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THE

AMERICAN NATURALIST.

Vol. XXXVIII. *January, 1904.* No. 445.

ADAPTATIONS TO AQUATIC, ARBOREAL, FOSSORIAL AND CURSORIAL HABITS IN MAMMALS.

IV. Cursorial Adaptations.

RICHARD SWANN LULL.

Of all portions of an animal's body to undergo specialization, those which have to do with locomotion show perhaps the most varied adaptations. Speed is so essential to a great number of forms, either for escape from the enemy or for the chase of prey, that its degree of development has much to do with the fitness of the creature for survival. This adaptation is most manifest in the modifications undergone by the feet and limbs, and to a less extent in the lengthening of the head and neck in long limbed forms as a necessary correlation. Speed adaptation is further shown in the moulding of the contour of the body to lessen the resistance of the air, an increase in the capacity of the heart and lungs to meet the more rapid expenditure of energy, and finally in saltatorial forms an increase in the length and weight of the tail.

Most terrestrial mammals can run; but in comparatively few orders is there any special adaptation for speed. Offensive flight

occurs among predaceous mammals such as the carnivorous marsupials and the true Carnivora, while defensive flight is found among herbivorous forms both among the marsupials and in the placental orders Rodentia, Perissodactyla, and Artiodactyla.

Feet and Limbs : — The main foot adaptations are shown in the passage from a primitive plantigrade to a digitigrade or to an unguligrade condition, and in the reduction of the number of digits ; the last being often accompanied by a close apposition or even by a fusion of the remaining bones of the metacarpus or metatarsus, and a reduction of the number of bones in the wrist and ankle. Cursorial adaptation leads to the formation of true ginglymoid joints in the carpus and tarsus, the motion being limited to flexion and extension though the angle of movement is increased. This motion is confined to the proximal podials, while the distal ones become flat and may either fuse with each other as in the Pecora, or with the metapodials as in the Tragulidæ. The development of tongue and groove joints mars the efficiency of the limb for other purposes than running.

The laws which govern digital reduction among vertebrates lead to an interesting grouping of the Mammalia with the Amphibia in which the order of reduction is first digit I then digit V as contrasted with the Sauropsida, the reptiles and birds in which the fifth digit is invariably the first to disappear, followed by digit I.

The axis of the mammalian foot may lie in digit III as in the perissodactyls and in most rodents though not in the Leporidæ ; between digits III and IV as in the Artiodactyla and Carnivora, or in digit IV as in the diprotodont marsupials.

Another marked cursorial adaptation is the increase in length of the lower leg and foot both absolutely and in relation to the length of the femur ; the lengthening of the limb increases the stride while the raising of its centre of gravity quickens the motion. This modification reaches its highest expression in creatures of moderate size such as the medium sized antelopes for in larger animals the increase in weight demands greater structural strength which limits the degree of such elongation.

The Carnivora whose need of cursorial adaptation, outweighed by a greater need of varied motion, is less than that of other

orders under consideration show the most generalized condition of feet and limbs ranging from the ancestral canid Cynodictis of the Oligocene and lower Miocene, in which both manus and pes are pentadactyl, though with functionless pollex, to Lycaon in which structural tetradactyly prevails. In most of the Canidæ the digital formula is manus 5, pes 4; the former being however functionally tetradactyl. A curious reversional condition is seen in many high bred domestic dogs in which a functionless hallux is present without skeletal connection with the rest of the pes, similar to the dew claws of cattle. The author has invariably observed this hallux claw in Saint Bernard dogs since he first noticed it, and it seems to occur in about fifty per cent. of fox terriers. Occasionally it is observed in other breeds but not so constantly and it probably never occurs in low bred individuals. I have recently observed a Saint Bernard with *two* hallux claws on each hind foot. Cats, with the exception of Cynælurus, the hunting leopard, are not addicted to running, as their run consists merely of a series of bounds, the creature slowing down as soon as possible, hence special cursorial modifications are hardly to be looked for outside of the genus mentioned. In Cynælurus the compact feet, poorly retractile claws and dog-like proportions and musculature show an interesting case of convergence toward the Canidæ.

As in Lycaon the hyænas have also reached a condition of structural tetradactyly, the most extreme case of digital reduction to be met with in the order.

Among the polyprotodont marsupials the Tasmanian wolf, Thylacinus, which lacks only the hallux shows thus the same digital reduction as in the majority of Canidæ though the feet are much less specialized. The diprotodont marsupials on the other hand exhibit extreme modifications both for running and jumping.

Of the diprotodont marsupials the Peramelidæ, the bandicoots, exhibit decided cursorial modifications. Disparity of size exists between the fore and hind limbs, and there is aside from this fact a further kangaroo-like reduction of the pes. The hallux is very much reduced; digit IV is on the contrary the dominant one, while digits II and III are syndactylly united to offset

digit V. In Peragale the lateral digits, except the hallux, are subfunctional while in Chœropus the pes is functionally monodactyl although not structurally so. The manus of Peragale has five digits the three median ones being functional, with III as the dominant finger, while the external digits are functionless. The ungal phalanges on II, III, and IV are long and deeply cleft. In Chœropus digits I and II are reversional, digit IV being vestigial, while II and III are functional, III being as in Peragale, the dominant one.

From the digital modification observed in the Peramelidæ to that of the kangaroos is but a step, for while in the latter the manus is more generalized the pes has reached a higher degree of specialization in the total reversion of the hallux, the plan of modification being precisely as in the bandicoots. The more generalized pentadactyl manus, which shows no cursorial modification, would seem to indicate that the bipedal gait was acquired before speed requirements were met.

The Rodentia have five or six families in which true speed adaptation occurs; one, the Leporidæ, which have a combination of cursorial and saltatorial gait, the Dasyproctidæ and Caviidæ which are purely cursorial, and the Dipodidæ and Pedetidæ which are saltatorial.

In the Leporidæ, the hares and rabbits, the gait is a curious mixture of leaping and running. The wood rabbit, *Lepus sylvaticus*, when in a full gallop progresses in a manner similar to that of most quadrupeds, while the jack rabbit, *Lepus campestris*, which is a true hare, moves by a series of bounds, irregular in length, with all of the limbs moving synchronously, though the weight borne upon the fore limbs must be very slight, the powerful hind limbs giving the impetus to the body. The Leporidæ show no especial digital modification other than the simple reduction of the hallux. There is an elongation and greater compactness of the metapodium as in the Canidæ among the Carnivora, and the axis of the foot lies between digits III and IV.

Of the purely cursorial types the Dasyproctidæ are the more generalized though they exhibit two distinct stages in the reduction of the digits. The first is that of Cœlogenys, the paca, in which the manus and pes are both structurally pentadactyl

though the pollex is reduced, while in the foot but three digits are functional, the lateral digits being vestigial.

In Dasyprocta, the agouti, however, the hand remains distinctly pentadactyl though digits I and V are subfunctional, while in the foot the digits are reduced to three. Thus the foot is both structurally and functionally tridactyl, the metatarsals being closely pressed together though not fused. The compact pes thus formed is tending toward that possessed by the Dipodidæ (*vide infra*).

The Caviidæ, represented by the Patagonian cavy, Dolichotus, show a further reduction over Dasyprocta in that in the former the manus is tetradactyl while the pes is in the same stage of reduction in each.

Among the truly saltatorial rodents a range of specialization is shown, starting from Perodipus, in which the manus and pes are each pentadactyl though there is considerable disparity of size between the fore and hind limbs, the progression being by leaping with the hind feet. Dipodomys, the kangaroo rat, belonging, together with Perodipus, to the American family Heteromyidæ, has much the same proportions, but the pes is tetradactyl. In Pedetes, the African jumping hare, the pes is tridactyl, the median digit being much the longest; while in the true jerboas, as Dipus, the disparity between the limbs reaches its greatest development and the elongate metatarsals are fused into one very bird-like bone. The digital formula is manus 5, pes 3; but the clawless pollex is evidently undergoing reduction.

Among the ungulates I know of none in which cursorial adaptation is manifest, which have not already functionally lost the pollex and hallux, that is with the exception of Phenacodus among the condylarths which was pentadactyl and undoubtedly could run though exhibiting no very marked cursorial adaptation. In general, while the pes is often more specialized than the manus there is far more uniformity in the plan of modification of fore and hind feet than was observed in the rodents and diprotodont marsupials. The artiodactyl and perissodactyl stems have modified the feet in such different ways that it becomes necessary to give each group separate treatment.

Among the Perissodactyla, the rinocerotine group, mostly of

unwieldy build, contains but one family, the Hyracodontidæ, ranging in North America from the Bridger to the White River, in which a running type developed. Here the manus is tetradactyl, the pes tridactyl, and as Osborn[1] says: "Tridactylism is rapidly acquired with a tendency to monodactylism in the lower Oligocene." They strongly suggest the primitive horses in general contour.

The Equidæ are too well known to require more than a brief review. The pentadactyl ancestral form is as yet undiscovered and must be looked for in the Cretacic, for in the lower Eocene there appears Eohippus with a tetradactyl manus, the pollex being represented by a splint, and a tridactyl, elongated pes which bears a splint of digit V. The other Eocene horses exhibit the same stage of digital reduction as in Eohippus; but Mesohippus of the middle and upper Oligocene is tridactyl in the manus as well as in the pes, the fifth digit of the former showing a splint-like metatarsal, digit I being vestigial. Here all of the digits are functional the laterals finally losing their contact with the ground in Merychippus of the middle Miocene and in Neohipparion of the upper Miocene, a beautiful specimen of which has lately been added to the American Museum collection. Hypohippus of the middle Miocene with subfunctional lateral digits and, in the manus, the vestige of metacarpal V is an instance of arrested evolution owing probably to marsh dwelling habits which necessitated a spreading foot.

Finally the monodactyl type of the Pleistocene and Recent is represented by the genus Equus in which digits I and V are reversional and digits II and IV vestigial, being represented by the metapodial splints alone.

The Equidæ are curiously paralleled in foot reduction by the South American Litopterna in which the tridactyl condition with functionless lateral digits is shown in Proterotherium from the Santa Cruz formation, Lower Tertiary of Patagonia. This creature seems to parallel Merychippus, the main distinctions being that the former has rather more slender phalanges in the middle digit while those of the lateral digits are proportionately

[1] Osborn, H. F. The Extinct Rhinoceroses of North America. *Mem. Amer. Mus. Nat. History*, Vol. I, Part 3, p. 93.

more robust. The metapodials are shorter and stouter than in the horse, those of digits II and IV particularly being much more prominent.

Thoatherium from the same beds is monodactyl, the lateral metapodials being even more vestigial than in Equus which it parallels, and as in Proterotherium, the phalanges, especially the proximal and ungal of the remaining digit are much more slender than in the horse, the ungal being cleft. A curious admixture of perissodactyl and artiodactyl characters is seen in the feet of the Litopterna for they have the odd toed feet of the Perissodactyls together with the characteristic double tarsal joint, though not to so great an extent, of the artiodactyls.

The Artiodactyla early lose the hallux and pollex, for except in Oreodon and Agriochœrus we have no instance of their survival and while digits III and IV are equally well developed, II and V suffer all degrees of reduction from that seen in the swine to the total disappearance in the camel and Antilocapra.

The swine are four toed, the lateral digits being sub-functional. Dicotyles, the peccary shows an advance over most Suidæ in that digit V of the pes is entirely wanting giving an asymmetrical foot, of uncommon occurrence in the order though found in the Anoplotheres as well. In Dicotyles the metacarpals are slightly fused at their proximal end while in the metatarsals the fusion extends over half the length of the bones. The Pleistocene genus Platygonus shows a still greater specialization as it is structurally didactyl, but a splint of the fifth metatarsal remaining. The metapodial bones show a greater degree of fusion than in Dicotyles.

The Tragulidæ or chevrotains are in a sense transitional between the swine and the true deer for, while four toed, the lateral toes are functionless although in the existing genera Tragulus and Dorcatherium (Hyomoschus) the lateral metapodials are entire. Fusion of the median metatarsals to form a canon bone is found in Tragulus, but not in Dorcatherium which together with its somewhat better developed lateral digits presents a more generalized condition than does Tragulus. Gelocus, an extinct form ranging from the Eocene to the Oligocene, is more specialized than either of the existing genera in that the

lateral metapodials are incompletely ossified. The metacarpals are not fused, while the presence or absence of fusion of the metatarsals is a specific variation.

The extinct Oligocene genus Protoceras gives us an interesting example of the acceleration of the specialization of the hind limbs over the fore, for while the latter have four well developed functional digits those of the former are reduced to two only, with closely applied metatarsals which do not fuse, though strongly tending so to do. The lateral metatarsals are represented by proximal vestiges only.

In the Pecora or true deer the lateral digits are reduced, being functionless in most genera though sub-functional in Moschus and in Rangifer probably due, in the latter genus at any rate, to the necessity of a broad plantar surface for support on the mossy tundras or on the snow, a condition analogous to that of Hypohippus among the horses. In the deer the lateral metapodials are incomplete, their distal ends always occurring while only in certain genera as Cervus and Cariacus are the proximal extremities also retained.

The Bovidæ exhibit an almost complete reduction of the lateral digits, the dew claws being dermal appendages only, the proximal phalanges being invariably absent, while the final stage of total reduction of the lateral toes is found in the camels, the giraffe, and in Antilocapra. In the Bovidæ as well as in the later Camelidæ and the other forms mentioned the fusion of the metapodials to form a canon bone is complete.

In the later camels there is a retrograde descent from the unguligrade to the digitigrade condition, wherein the phalanges lie prone upon the ground, giving the characteristic broad, pad-like foot of the modern camel.

There are no instances of saltatorial adaptation among the ungulates though some antelope and deer are wonderful jumpers.

The lemurs among the primates present several instances of saltatorial adaptation, notably in the sub-family Galagininæ and in Tarsius, family Tarsiidæ; but here instead of an elongated metatarsus, which has been the rule heretofore, it is the tarsus which is modified, for the calcaneum and navicular become

lengthened and cylindrical as do the calcaneum and astragalus in the frog. The hallux is large and opposable while digits II and III are somewhat reduced, digit IV being the longest. In Tarsius digits II and IV are clawed while the others bear flattened nails.

The Skull.— Cursorial adaptation has its effect upon the skull only in the correlation that exists between long limbs and dolichocephaly, brought about by the necessity of reaching the ground on the part of a grazing animal. This is strikingly illustrated in the horse series where the increase in the length of the skull parallels the lengthening of the limbs.

Saltatorial forms which, like Dipus, have lengthened the hind limbs only, do not exhibit marked dolichocephaly, as the feeding habits of the creature do not require it. The grazing kangaroos however have a moderately elongate skull.

The Vertebral Column.— Cursorial adaptation among mammals is shown in the lengthening of the cervical vertebræ, especially in dolichocephalic forms, strikingly illustrated by the giraffe and by Alticamelus of the Loup Fork of Colorado[1] a camel showing the most remarkable convergence toward the giraffe, although the latter is derived from a totally different stock.

Among the saltatorial forms, especially those with brachycephalic skulls, the tendency is toward the shortening of the neck accompanied by a greater or less degree of immobility. In Pedetes cervicals 2 and 3 are so closely articulated as to eliminate motion, in Perodipus the axis and the next two vertebræ are fused, while in Dipus all of the cervicals except the atlas are coössified as in whales. There is no increase or diminution in the number of cervicals as a result of speed adaptation. The dorso-lumbar series seem to suffer little alteration in cursorial forms, though the lumbars increase in size in saltatorial types. The high number of vertebræ found in the horses is also found in other perissodactyls and in the Proboscidea, and so is not to be considered a modification coming within the scope of the present discussion. In some saltatorial forms, as the jerboas, an exceedingly short back is found; but saltatorial adaptation can exist without this feature.

[1] Matthew, W. D. *Mem. Amer. Mus. Nat. History*, Vol. 1, Part 7, p. 429, pl. XXXIX.

The tail is generally reduced as a result of cursorial adaptation, though in coursing dogs, as the grayhound and pointer, it aids in keeping the balance when the creature changes its direction and this may be a secondary cause for its retention. In saltatorial forms on the contrary, the tail becomes an important organ for use as a counterpoise; for in truly saltatorial mammals the tail increases in length and in weight directly with the increase in proportion of the hind over the fore limbs. It is in such bipedal forms as the kangaroos and the jerboas that the caudal counterpoise reaches its highest expression, for in the former the tail is long and heavy while in the latter the somewhat less proportionate weight is compensated for by the extreme length of the organ and the tuft of hair at its tip. The tail of the African jumping hare, Pedetes, is long and feather-like, like that of a squirrel. The development of a caudal counterpoise in bipedal mammals is paralleled among dinosaurs of the Mesozoic though, as the author will show in a forthcoming memoir,[1] dinosaurs are never saltatorial, but always progress by alternating strides. This is what one would be led to infer, for whatever the increase in speed may be, I know of no reptile which runs at a gallop that is with each pair of limbs moving nearly in unison, while among the mammalia this is the common method of rapid progression. The jerboas *walk* on the hind limbs with alternate strides, *hopping* only when speeding while the kangaroos have lost the more primitive alternate footed gait and use the hop for all degrees of rapidity. The hop may thus be considered as a sort of bipedal gallop.

Among the struthious birds, the cursorial habit evidently having been acquired after the loss of the reptilian tail, the counterpoising function is subserved by the wings which bear up the anterior part of the body and at the same time lighten the creature's weight.

Columbia University, Department of Zoölogy,
November 30, 1903.

[1] Lull, R. S., Fossil Footprints of the Jura-Trias of North America. *Mem. Boston Soc. Nat. Hist.* Vol. 5, no. 10.

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ON THE OSTEOLOGY AND SYSTEMATIC POSITION OF THE PYGOPODES.

R. W. SHUFELDT.

In a series of papers contributed to *The Journal of Anatomy and Physiology* of London (1889–1890) appeared a number of my drawings of the bones of pygopodine birds. Among these the osteology of certain grebes and loons was illustrated, but the material at hand then was meagre. Moreover, through an oversight the plate illustrating the bones of the lower extremity in the loons was omitted. The osteology of the pelvic limb in a loon is in a way more deserving of our consideration than perhaps other parts of the skeleton in those typical divers, and as I had fortunately preserved the aforesaid plate, I take occasion to publish it here.

In an article entitled "Concerning some of the Forms assumed by the Patella in Birds" (*Proc. U. S. Nat. Mus.* Vol. vii, 1884, pp. 324–331) I published two or three figures of the leg-bones in loons and grebes, but the descriptive text-matter had reference only to the morphology of the patella.

In the present memoir all of my previous work has been amplified and practically rewritten, while I have added my investigations upon the osteology of the Pygopodes.

In my classification of birds the Pygopodes appear in the scheme as a suborder, thus: —

Suborder: — PYGOPODES.

SUPERFAMILIES: —
- Podicipoidea.
- Urinatoroidea.
  - FAMILIES: —
    - Podicipidæ.
    - Urinatoridæ.

Newton in his classic 'Introduction' to his *Dictionary of Birds* (p. 111) makes the statement that the "group known as *Pygopodes* has been often asserted to be closely akin to the *Impennes*, and we have seen that Brandt combined the two under the name of *Urinatores*, but of their essential difference there can now be no doubt, and indeed it is hard to look upon *Pygopodes* as a natural group, so many are the differences between the *Podicipedidæ* or Grebes and *Colymbidæ*[1] or Divers, though recent morphologists agree to unite them, while the affinity of the Divers to the Auks seems to be still more uncertain, and there appears to be ground for considering the *Alcidæ* to be much modified relatives of the *Laridæ*."

The discovery of the toothed Hesperornithidæ of the middle cretaceous of America has doubtless modified the opinions of systematists regarding the affinities of the Pygopodes.

I agree then essentially with Fürbringer in confining the families Colymbidæ (loons) and Podicipidæ (grebes) to a group "Colymbo-Podicipites," and closely associating the latter with the families Enaliornithidæ and Hesperornithidæ in a Suborder Podicipitiformes. Therefore I can proceed to the consideration of the osteology of the grebes.

The Skeleton of the Grebes.

Grebes may have the superior osseous mandible longer than the cranium, or they may have it shorter than that part of the skull. Of the first-mentioned, *Colymbus holbœlli* is a good example, while *Podilymbus podiceps* exhibits the latter characteristic. In *C. holbœlli* the long, straight and acutely-tapering superior osseous mandible is fully one fourth longer than the cranium, and either narial aperture is suboval in outline, being equal in length to the end of the bill which extends beyond its anterior termination. This narial aperture is rather acutely holorhinal posteriorly, and the dentary margins are cultrate for

[1] "American ornithologists have lately used this term for the Grebes, to the great disturbance of nomenclature. It is apparently from the ancestors of the *Colymbidæ*, before they lost their teeth, that *Hesperornis* branched off as a degenerate, bulky and flightless form." — A. N.

their entire extent. No part of the nasal septum ossifies in the skull (a feature common to all grebes that we have examined). Each nasal bone has a form much as we find it in the loons, its processes being flat and rather broad. The region over the cranio-facial hinge is moderately concaved, where the nasal processes of the premaxillaries are seen to be persistent throughout life, and their sutures plainly visible in the adult.

Posterior to this space the frontals between the superior orbital margins are much narrowed, and the supraorbital glandular depressions barely discernible, being distinguishable in the dried cranium only along their posterior moieties. The external superficies of the cranial vault in the parietal region are smooth and rounded; the crotaphyte fossæ are extensive and practically meet, mesially, over the large rounded supra-occipital prominence, though no median crest or line stands between them. More laterally, and upon either side, the occipital crest is raised and prominent. In the grebe now under consideration it is quite as thin, and lamellar-form as it is in the loons.

Upon lateral aspect of the skull, the post frontal and squamosal processes are much absorbed, and the valley between them wide. The aural entrance is extensive, very open and exposed, being overarched by its somewhat thickened postero-superior border.

Either zygomatic bar is straight, transversely flattened, and tapers slightly as it proceeds forwards where it assists in making a schizognathous articulation with the other bones.

The interorbital septum is markedly deficient in bone, and the anterior cranial walls about the exit of the nerves hardly less so. This deficiency is even greater than it is seen to be in the loons. Pars plana is weak and feebly developed, and externally, it passes upwards and forwards to fuse with the nether aspect of the frontal. A transverse perforation may normally exist just posterior to the true mesethmoid. This latter ossification terminates rather abruptly in front by a broadish face with a small median crest extending down it as far as the sharpened anterior apex of the rostrum, over which it is carried forwards.

A lacrymal is a fair-sized bone with a very narrow superior limb, closely articulating with its entire mesial border with the

frontal and nasal, while the rather larger descending portion of the bone is plate-like, being transversely compressed, and does not reach the maxillary below. At its apex it supports a spiculiform os uncinatum, as we find in the Urinatoridæ.

The foramen magnum is large, looks almost directly backwards, and is of an acute cordate outline, with the apex above. The occipital condyle is well developed, completely sessile, and barely notched superiorly. Passing to the basitemporal area we find it somewhat contracted, nearly level and smooth, while its anterior apex underlapping the double entrance to the Eustachian tubes. There are no evidences whatever of basipterygoid processes, and the long, straight pterygoids stand well away from the sphenoid. One of these bones has cultrate inner and outer edges or borders, and is peculiar in the way it articulates with the quadrate. The latter bone throws out a well developed apophysis, mesially, the summit of which is rounded to be received into the articular cup existing on the posterior end of the pterygoid. In most birds the pterygoids articulate upon the inferomesial border of the os quadratum. These bones in the grebe hardly touch each other anteriorly, where their palatine heads are to some extent expanded. The sphenoidal rostrum is comparatively slender and is carried to a sharp apex in front. The palatines have their postero-external angles completely rounded off, while their lower inner and outer margins are moderately bent downwards,— the inner one rather abruptly so. When articulated *in situ* these bones are in contact with each other all along beneath the rostrum. The antero-mesial portion of the post-palatine part of the bone, curls upwards and inwards towards the mesethmoid, and in front its mesial process runs forward as a long slender spine for the accommodation of the vomer. The prepalatine portion of a palatine is long, narrow and vertically compressed. Extending a long ways to the front, rapidly tapering to a point as it does so, the prepalatine underlaps the maxillary and maxillo-palatine, and passes along close to the inner aspect of the dentary part of the premaxillary, being thoroughly fused there in the adult. The suture, however, remains visible throughout life. For the size of the bird, Holbœll's grebe has one of the longest vomers at present

known to me. It is lamelliform, thin and narrow, its surface being in the middle plane, while behind it is moderately bifurcated, to be carried to a sharp apex anteriorly. Either maxillo-palatine is a subconcavo-convex oval plate of bone, of some little size. Its mesial surface looks inwards and upwards, the anterior fourth being fused almost indistinguishably with the nasal, maxillary, palatine and premaxillary. Palatines and maxillo-palatines are well separated from each other in the middle line, and from the vomer.

An os quaratum is rather a large bone in the grebes, with a long, gently-inturned orbital process. Its mastoidal head supports two facets of articulation, being separated from each other by a shallow sublongitudinal valley. Transversely, the quadrate is much compressed, and I have already described above the process at its infero-internal angle to accommodate the hinder end of the corresponding pterygoid. The mandibular portion is much excavated centrally on its nether aspect, with a small articular facette on either side of the concavity. There is also an articular line bounding this depression posteriorly. The bone appears to be pneumatic.

Passing to the consideration of the mandible we find it to be of the very acutely V-shaped pattern, with the ramal vacuity completely closed in. The articular ends are enlarged and abruptly truncated behind, where they show each a flat triangular surface. The ramal sides posteriorly are thin, lofty and flat, to become narrower and thicker as they pass tapering forwards to the acute apex. The symphysis is short, slightly excavated above, and rounded below. It is only the posterior extremities of the mandible that are at all pneumatic, the usual pneumatic orifice being at the end of the inturned, stumpy articular termination of the bone. Aside from the brevity of the superior osseous mandible in the short-billed grebes, the skull characters as given above for *Colymbus holbœlli* are substantially repeated in them. In *Podilymbus podiceps*, however, I observe that the anterior extremity of the vomer terminates in a small, rounded, disc-like nib, and its quadrates are rather more delicately fashioned. It also has the mesial notch on the upper side of the occipital condyle, and a mid-longitudinal raised line on the supra-

occipital prominence, which, as we shall see, is so much better marked in the loons. Finally, the supra-orbital glandular depressions are hardly perceptible in these dabchicks.

Grebes possess a hyoidean apparatus in some respects peculiar. It is well exemplified in Podilymbus, where we find the glossohyal performed entirely in cartilage, and the first basibranchial represented by an expanded suboval disc of bone. At the hinder margin of this the short second basibranchial, as a delicate osseous rod, articulates in the middle line, while the long, slender cerato-branchials, one on either hand, articulate close to it. The epi-branchials are short and spiculiform. We find a somewhat similarly fashioned first basibranchial in the tongue of the kingfishers, but such a form of it is rare among birds.

The sclerotal plates in the eye-balls of the Podicipoidea have their usual ornithic characters, being of moderate size only, squarish in form, and overlapping each other in the ordinary manner.

The Trunk Skeleton in the Grebe.

Birds of this superfamily vary, even for the genera, with respect to the number of vertebræ in the spinal column, and the corresponding vertebræ themselves vary much in form and character. Species such as *Colymbus holbœlli* and *Podilymbus podiceps* have 19 vertebræ in the cervical region of the spine, the 19th bearing a pair of ribs that do not articulate by costal ribs with the sternum.

But *Æchmophorus occidentalis* has 21 vertebræ in the cervical region, with the free ribs on the 21st as they occur on the 19th in Podilymbus. This last mentioned species has the first four dorsal vertebræ fused into one piece, but the fifth one, standing between this piece and the pelvis is free, and its ribs articulate with the sternum by costal ribs. There is also a pair of pelvic ribs, the hæmapophyses of which do not usually meet the sternum. All have large epipleural appendages, save the last-named; they being even found on the cervical pair. They do not fuse with rib borders.

In Æchmophorus the dorsal vertebræ do not fuse, although

the interarticulations are very close. This grebe has *two* pairs of pelvic ribs, the hæmapophyses of the first pair reaching the costal borders of the sternum. All grebes have large hypapophyses on the last two or three cervical vertebræ, and on all the centra of the dorsal vertebræ; they are very large in Æchmophorus, the first two being represented by flattened and out-spreading discs of bone of an irregular form. This species is also peculiar in having the neural spines of the 19th, 20th and 21st vertebræ much modified for muscular attachment. They resemble the ploughshare in form, being greatly increased in size, and the excavation occurring behind. The first (19th) has this modification most pronounced, while it is least marked in the ultimate one (21st). Parapophysial spines are quite aborted, or are represented by mere nibs of bone. Æchmophorus has the hypapophysial carotid canal extending through *twelve* vertebræ; it being generally closed in completely on the 9th and 10th one of the series. These vertebræ are the 4th to the 15th inclusive.

In *Podilymbus podiceps* I found 49 vertebræ in the spinal column. Nine free vertebræ and a pygostyle compose the tail of this bird, and when they are articulated *in situ*, they form a peculiar sigmoid curve, dipping downwards, then upwards, as the letter S. The pygostyle is very small and its characters much aborted.

Grebes have their caudal vertebræ considerably compressed in the transverse direction. In the dorsal region the tendons of the spinal muscles ossify and fuse with the summits of the neural spines of the vertebræ, and metapophysial spiculæ may also occur upon the transverse processes, as we find them in other water birds. Another thing is worthy of attention here, and that is the general form and outline of the skeletal parietes. Further along it will be seen that in the auks and puffins this is elongated,— the sternum being long, and the ribs sweeping far backwards beneath the pelvis. In the grebes this is not usually the case, for in Podilymbus the form of the thoracic skeleton is much as we find it in the gulls; in Æchmophorus, however, it is again more as in the Alcæ; it is quite so among the loons.

The form assumed by the pelvis among the Podicipoidea is

noteworthy; though in its general pattern it closely approaches what we find in the Urinatoridæ. The pelvis in *Æchmophorus occidentalis* well exhibits all the characters of this compound bone among the podicipidine types. In that species is much elongated and compressed laterally, especially its pos-acetabular portion. In front of the acetabulæ the fused sacral crista rises far above the fore part of the ilium on either hand,— which latter, each have the form of an oar-blade with a squarely truncated anterior extremity. An extensive antitrochanter surmounts either cotyloid cavity, while posteriorly the post-acetabular surface faces almost directly outwards. Along the dorsal middle line, for the posterior third, of the pelvis the iliac borders are closely pressed together, marking the uro-sacral vertebræ. Behind, a deep cleft indicates the division which originally marked the terminal point of union between the ilium and the very long and narrow ischium. The obturator foramen completely merges with the obturator space, and the much-extended, flat, ribbon-like post-pubic rod is widely separated from the lower ischiac border, being carried far back almost opposite the pygostyle. The ends of these bones of the pelvis, however, are not dilated as are the postpubic bones in the loons. The ischiac foramen is large, and of an elliptical outline. Podilymbus presents almost the same pelvic characters as those just described for Æchmophorus, and in this species the os innominata fuse completely with the "sacrum,"— though posteriorly the superior iliac margins do not quite meet over the uro-sacral vertebræ.

The sternum is very characteristic. In Figures 1, *a* and 1, *b* I have drawn it for *Colymbus nigricollis californicus* where its podicipidine features may be seen. Generally speaking it is broad and short, with a large subelliptical notch cutting out its xiphoidal portion on either side of the keel. This gives rise to a pair of flaring external xiphoidal processes, which curve outwards, then inwards, extending rather beyond the mid-xiphoidal prolongation. They are long and narrow in the short-billed grebes, and broader and relatively shorter in Æchmophorus and Colymbus. The mid-xiphoidal process always shows a triangular notch, which is much deeper in Podilymbus than in other species,

and it may also show certain foramina in the hinder part of the sternal body. The keel is triangular with a somewhat acute carinal angle produced in front, and closely approached by the os furcula when the bones of the shoulder-girdle are articulated *in situ*. Usually *six* articular facettes are found upon either costal border, and a costal process is large and subtriangular. No manubrium exists, and the bone is depressed where it occurs in the sternum when it is present. The costal grooves are noteworthy, for they are very deep, and their superior and inferior borders are produced well forwards.

As in the rest of the skeleton, save the hinder part of the skull and lower jaw, the sternum in the grebes is completely non-pneumatic.

Upon comparing the sterna of our various species of grebes, I find but few characters of marked difference beyond the matter of size. *Colymbus auritus* possesses a sternum most like that of *Podilymbus podiceps*, and next to it, in that respect, comes *Colymbus holbœlli*.

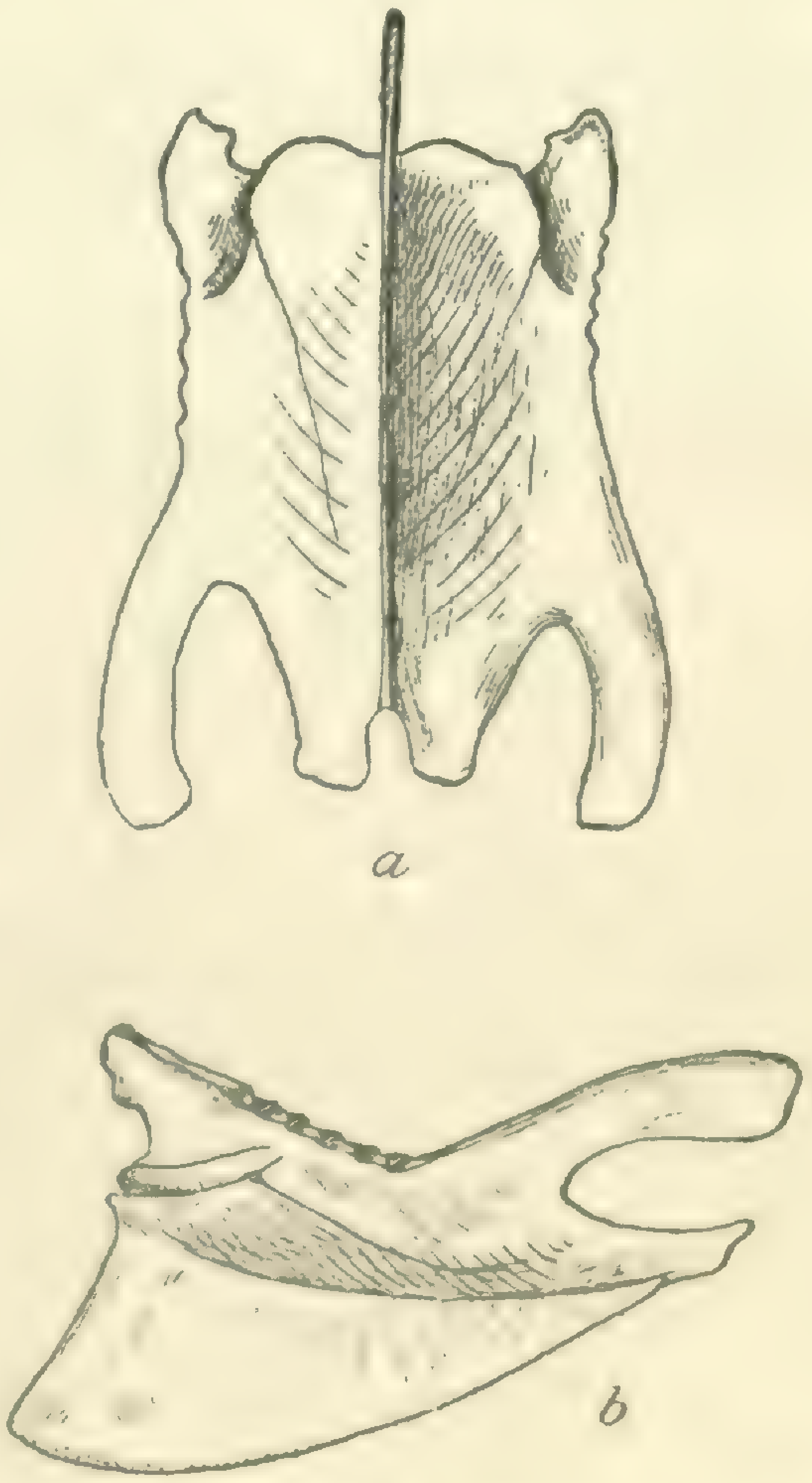


FIG. 1. *a*. Sternum of *C. n. californicus* from below; *b*. left lateral view of the same bone. Natural size.

In the several bones of the shoulder-girdle, — the salient characters are the same for the various species of this group. The os furcula is always found to be of the broad U-pattern, much bowed to the front, without hypoclidium (*C. n. californicus*), and with narrow, laterally compressed limbs. Superiorly, the clavicular limbs taper out to acute points, and when the elements of the girdle are articulated *in situ*, one of these rests by its outer

aspect against the head of the corresponding coracoid, while the apex passes far over the anterior end of the scapula. Thus a piece of the clavicular end, including the apex, is above the scapula but not being in contact with it; — the actual point of contact between these two bones being several millimeters beyond or anterior to the apex.

The scapulæ are quite long, and narrow, being gently curved throughout their length in the vertical plane, the convexity being along the dorsal aspect. For the most part the bone is of uniform width, the head alone being somewhat thickened. It offers only a moderate articular surface for the coracoid, and the os furcula rests upon its upper side.

The scapulæ are especially slender in *Colymbus auritus*. Comparatively speaking, the coracoids are usually long and not very stout; they may, however, be only of moderate length. The summit of one of these bones offers us the usual ornithic characters, being peculiar only in having such a small scapular process, and being rather compressed laterally. The distal end of the bone is dilated and much flattened in the antero-posterior direction. This expansion is carried some distance up the outer side of the shaft, and, owing to the fact that the sternal end of a coracoid sets so deep in its articular groove in the sternum, the corresponding articular surface on the bone is carried up some little distance both in front and behind,— most so upon the latter aspect.

When the bones of the shoulder-girdle in a grebe are articulated as in life, there is quite an interval between their sternal ends, mesiad. As I have said above, this interspace on the sternum is concave and its convexity is coextensive with the inner border of the coracoid upon either side. A wide interval in the same location exists in *Hesperornis regalis*, the great diver of the Cretaceous epoch in America.

The Appendicular Skeleton of the Grebes.

As an example of the skeleton of the pectoral limb of an adult specimen of *Colymbus holbœlli* we have chosen No. 17815 Coll. U. S. Nat. Mus. In this specimen the humerus is 10.6 cms. long, with nearly a straight, subcylindrical shaft, the extremities

of which are but moderately enlarged. At the proximal end the radial crest is seen to be much reduced, and the excavation overshadowed by the low ulnar crest which is unusually shallow, with no evidences of pneumatic orifices. The articular surface of the humeral head has the ordinary avian character. Distally, the oblique and ulnar tubercles are prominent and offer considerable articular surface for the antibrachial bones. The ulna is 10.2 cm. in length, and considerably compressed subtransversely; the long, slender radius when articulated, *in situ*, with it, is in contact with its shaft for its distal moiety, thus much reducing the "interosseous space," which, in reality, only exists proximally. Manus has a total length of 8.3 cms., and the two usual free carpals are present in the wrist. Carpo-metacarpus is peculiar in being so comparatively long and slender, and for having the index and medius metacarpals so close together, and so nearly parallel. The phalangeal digits are long and slim, and I fail to find any "claws" upon the distal extremities of any of them. The proximal phalanx of the index digit is also elongated and remarkably narrow; the expanded portion and digital shaft being indistinguishably merged with each other.

The skeleton of the wing in *Podilymbus podiceps* has the same essential characters as in the wings of the long-billed grebes. In all, the bones are well-proportioned and harmonize in their lengths and calibres with the bones of the pelvic limb, in any given species.

Altogether one of the most beautiful adaptive structures is the pelvic limb of a grebe. When properly articulated, the short femur has its long axis directed from the acetabular center, downwards, outwards, and slightly backwards. By the structure of the knee-joint this brings the long axis of the tibio-tarsus almost parallel to the long, mesial axis of the pelvis. Now the tibio-tarsal articulation permits the exact play of the foot, by a fore and aft motion, at right angles to this long axis of the tibio-tarsus. It is an avian oar. The tarsus is compressed to the last degree consistent with strength, — so that when it and its blade-like toes make the forward stroke, the minimum amount of podal surface is offered to the water in resistance. But in the backward stroke of the foot, the articulation permits of the

reversal of this act, and the toes being turned, and to some extent the tarsus, the maximum amount of surface thus afforded is brought into play as in an oar. Femur and tarso-metatarsus have about equal lengths, and they each equal *half* the length of the leg-bones, measuring from the apex of the patella to the mid-lower point of the arc of the distal tibial condyles (*Podilymbus podiceps*). The mid-anterior toe in the adult measures 5.5 cm. and the tarso-metatarsus only 3.8 cm.; these are about the usual proportions.

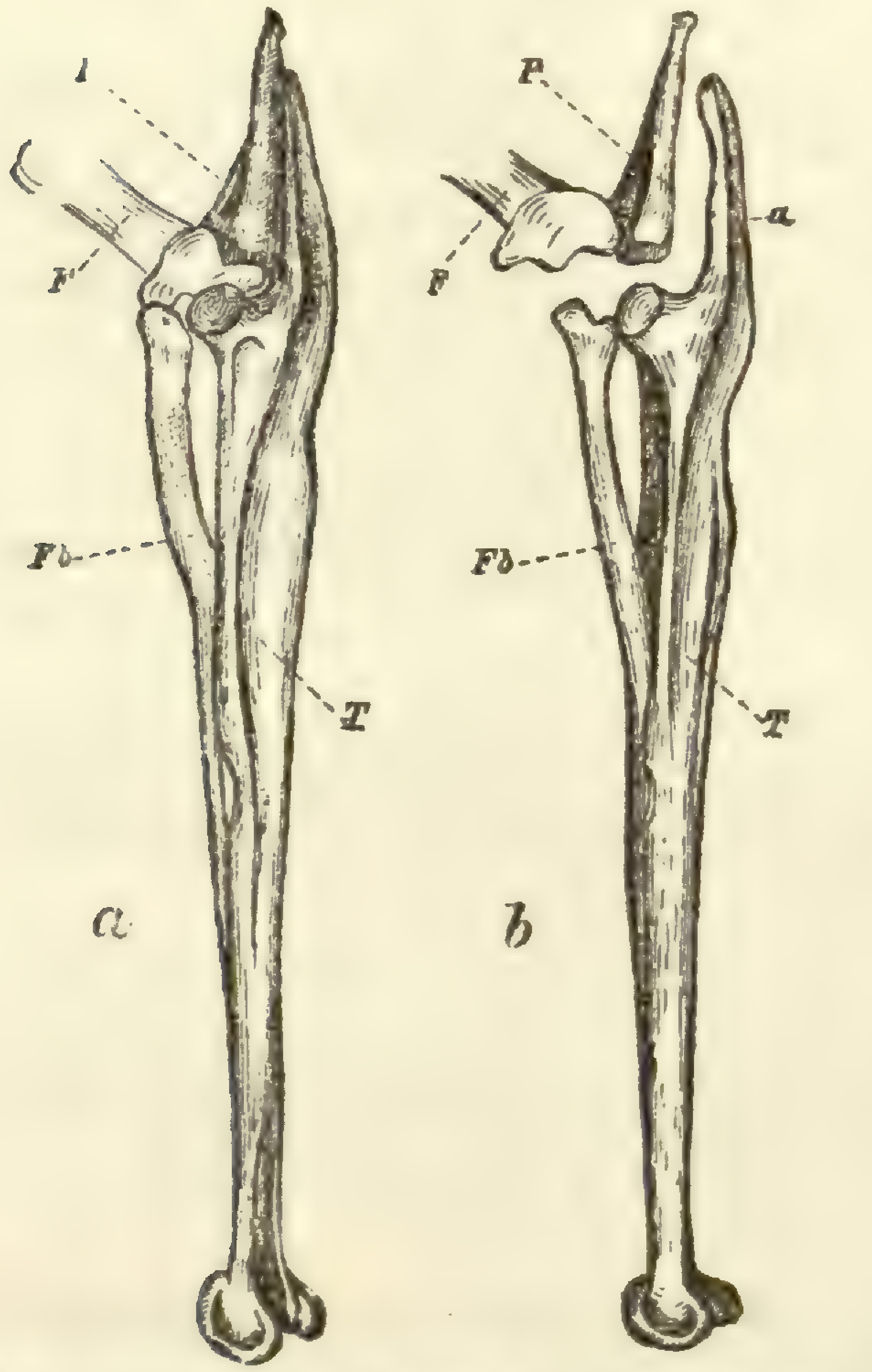


Fig. 2.—Leg-bones and patella of *Colymbus auritus*. *a*, the limb rotated slightly outwards; *b*, a square lateral view. In *a* the bones are *in situ*; in *b*, femur and patella are thrown backwards out of position. *a* rotular crest of tibia. P, patella; F, femur; *Fb*, fibula; T, tibio-tarsus. Natural size.

The head of the femur is large, and much excavated for the round ligament. At the summit the articular surface is rounded, and the trochanter does not rise above it. Its shaft is very slightly bowed to the front, and its condyles markedly prominent behind, with an unusually distinct and gaping cleft for the head of the fibula.

One of the most important characters of the tibio-tarsus is the upward extension of its cnemial crest, which is carried up to an apical process considerably above the summit of the shaft, but in direct line with the forepart of it. A large patella backs this at its supero-external aspect. It has something of the same form as the cnemial crest, above which it is slightly extended when articulated *in situ*. The procnemial ridge of the tibio-tarsus is extended as a sharp border down the

shaft of the bone; the latter being straight, flat anteriorly and rounded behind. Having the usual ornithic form, the tibial condyles are set rather obliquely on the distal end of the shaft. They are about parallel to each other. The fibula is very long with its lower end fused with the side of the shaft of the tibia. Superiorly, it is broad and flattened in the antero posterior direction, and stands well away from the tibial shaft (Figs. 2, *Fb.*).

Among the short-billed grebes the transverse compression of the shaft of the tarso-metatarsus is not nearly so evident as it is in such species as *Æchmophorus occidentalis* and *Colymbus holbœlli*. Moreover, in the dabchick there is a very slight twisting of the shaft upon itself, and this I have not observed in other grebes, either fossil or recent. At the summit of the bone, the articular excavations for the tibio-tarsal condyles are deeply sculpt, and the inner lateral border of the internal one may be conspicuously raised (Podilymbus). The subcubical hypotarsus of the tarso-metatarsus in most all grebes is deeply once-grooved in the mid-longitudinal line behind; and in front of this groove it presents one complete cylindrical perforation (also for the passage of tendons) with a similar, though smaller, perforation upon either side of it, situated more posteriorly.

This is quite different from what we find in the loons (see Fig. 18, of the Plate). Of the distal trochleæ the middle one is the lowest on the shaft; the outer one next; while the inner one is very distinctly elevated. They are all more or less drawn towards the rear aspect of the bone. The hallux digit is feeble and flake-like, as is the small, free metatarsal to which it is attached. It is considerably elevated upon the shaft.

Generally, the podal joints show more or less compression, while the terminal or ungual ones are positively scale-like, and, as it were, greatly flattened. Usually, the basal phalanges are the longest, and the others in any toe gradually diminish in this particular proceeding towards the extremities. Their arrangement as to the number on each toe is upon the more common ornithic plan of 2, 3, 4, 5 to the 1–4 toes respectively.

The Skeleton in the Loons.

In all of its essential characters, the skull of the loons agrees with that of the grebes. In the present description I have chosen the skeletons of *Urinator imber* and *Urinator lumme*,—the first being the bird known all over the world as *the* loon, the second, also a largely cosmopolitan type, is the red-throated loon or diver. In the latter the superior osseous mandible is fashioned upon the same plan as we found it in the long-billed grebes; it differs principally in curving very gently upwards, a feature not present in the beak of *U. imber.* The culmen in both species is convex and evenly rounded. Loons have the cranio-facial region depressed, best seen in *U. imber*, where the sutures between the nasal processes of the premaxillary and the nasals remain more or less open throughout life.

All the Urinatoridæ are holorhinal, and the dentary process of the nasal dips downwards and forwards in a gentle curve, thus including the large and somewhat elliptical osseous nares. They are devoid of any osseous nasal septum. Each lacrymal articulates to a very limited extent with the corresponding frontal, and almost entirely with the outer margin of the nasal. The os uncinatum at the inferior apex of its descending limit, fuses with that bone, but the lacrymal does not reach down to the maxillary in *U. lumme*, although it often does so in *U. imber.* In many of the gulls this process is much shorter, and is bent backwards and often anchyloses with the pars plana; in the Urinatoridæ the pars plana is not ossified, and the mesethmoidal plate is thin, showing a raised welt at the usual site of the base of this wing where it occurs in other groups.

A large vacuity is seen in the middle of the interorbital septum, but the optic and other foramina usually retain their integrity. The track of the olfactory nerve is commonly roofed over for its posterior third or more by an extension of the bony wall which covers the anterior aspect of the rhinencephalon. This arrangement is not seen in a specimen of the skull of *Larus glaucus*, and its interorbital septum is thick and entire.

The quadrate has a long, plate-like, and upturned orbital proc-

ess, and two prominent facets upon its mandibular foot, at about the same level.

Regarding the skull of any of the Urinatoridæ from above, the most striking features are the deep, sharply-defined, supraorbital glandular depressions. These are extensively perforated by minute foramina over their posterior halves, while a large irregular foramen occurs at each anterior end. Over the frontals they are separated by a thin crest of bone in the median line, while their posterior halves curve regularly outwards, to extend upon each roof-like post-frontal projection. In *U. imber* we find them giving rise to a raised superior orbital margin, connecting the lacrymal and the aforesaid post-frontal projections, as in Alca and Uria. In *Urinator lumme* this rim is sometimes incomplete. Fully as marked as these supraorbital depressions are the extraordinary crotaphyte fossæ. These are very broad antero-posteriorly, and strongly-marked throughout. On the top of the skull they are separated by a raised median line of bone, being the simple backward extension of that smooth central area of the vault, which has remained unmutilated by depressions. From this these fossæ sweep on either side in increasing depth downwards and forwards beneath the overhanging post-frontal roof and over the top of the external auditory wing.

In a specimen of *U. imber* belonging to the U. S. National Museum (No. 18256) I find the superficies of the superior orbital margins very much roughened. In the middle line there is also a "parietal foramen" at the hinder termination of a longitudinal gutter that extends as far forwards as the thin crest dividing the supraorbital glandular depressions.

Viewing the skull of the red-throated diver from behind we find that the large dome-like supra-occipital prominence is overlapped by these broad crotaphyte fossæ, and the median line separating them is extended directly backwards as far as the superior margin of the foramen magnum. This prominence is also transversely crossed about its middle by the raised crest that separates the crotaphyte fossæ from the occipital area. The plane of the foramen magnum is nearly vertical, and the reniform condyle projects directly backward from a thick-set

pedicle, its convex surface being inferior. We shall see further on that this posterior aspect of a diver's skull resembles much less the same view of the skull of any of the Laridæ than Alca does; indeed, the posterior view of the skull of the razor-bill very closely resembles a like view of the skull in several of the gulls.

On the under side of the skull of *Urinator lumme* we find the arrangement of the palate and other elements agreeing in all essential particulars with the gulls, auks, or guillemots; in other words, its structure is that of a typical cecomorph of Huxley's classification, so far as these parts are concerned.

In a well-cleaned skull the palatines can easily be traced to their anterior endings, and this is equally true of *U. imber.* Behind they are long and narrow, showing a double carination with a concavity dividing them. This is again divided by a transverse ridge near the middle of the body of each bone on its under side. The ascending processes of the palatines are embraced by the hinder ends of the vomer, and between them both rides the thin inferior edge of the rostrum. Anteriorly the vomer among the Urinatoridæ is more or less pointed, while above it is longitudinally grooved for its entire length, and the edges of this groove are well curled outwards.

The maxillo-palatines are thin concavo-convex plates raised above the horizontal portions of the maxillaries, and otherwise arranged as in the Alcidæ and Laridæ.

The posterior heads of the palatines are in contact, and form a groove between them above for the rostral bar of the presphenoid. They are embraced in a peculiar manner by the anterior ends of the pterygoids, which are fashioned like little two-toed feet to hold them, the larger claw being above and the smaller one below, the seizure being of such a nature as to limit the motion to a fore and aft one. Coues noticed this arrangement in the loon, and alludes to it in his memoir. The posterior end of each pterygoid is much enlarged and makes an extensive articulation with the quadrate of the corresponding side.

The foramen ovale opens laterally in the red-throated diver, and still more so in the loon, and the posterior wall of each orbit is marked by an outwardly concave, nearly vertical ridge, which

seems to limit the depression of the crotaphyte fossa upon that aspect on either side. Among these divers the mandible is very much alike.

It is shaped so as to be in harmony with the form of the superior one, being carried to a sharp point anteriorly. Opposite to the posterior ends of the dentary each ramal side is deep from above, downwards, and the vacuity found in other birds upon this surface is completely closed in by the mandibular elements of the vicinity — the splenial and dentary — principally the latter.

As among the Alcidæ, however, we find a large elliptical foramen in the surangular in most divers, but rather a small one in the loon in the same situation. Both the upper and lower ramal borders are rounded and the coranoid processes fairly well developed.

Viewed from above, we find the mandible to be V-shaped, with rather a short symphysis. The articulate facets for the quadrate are large and included in a squarish area in each mandibular end. Each angle is truncate from above, downwards and backwards, its emarginated lateral borders behind, enclosing a rather deep concavity, seen upon direct posterior aspect. Now the outer of these two borders on either ramal angle is produced upwards, forwards, and outwards as quite a prominent peg-like process. Thus I consider the angles of this mandible as being both truncate and recurved, and it is easy to conceive how by gradual steps this condition in the Urinatoridæ could be so modified as to have the truncation subordinated or even disappear, while the process became the feature of the mandibular angle, as in such a form as *Lunda cirrata*, wherein but little further change is required to produce the process as found in the Gallinæ. The mandible of *Larus glaucus* before me has no such process, and the parts that give rise to it are not present, the mandibular ends being reduced to their simple requirements for articulation with the quadrates.

The skull and mandible in the Urinatoridæ are non-pneumatic, though apparently not always so in *U. imber*.

I regret very much to find that the hyoid arches belonging to the skeletons of these divers in my hands have been unfortunately lost, and I am unable to say anything about their struc-

ture in these birds from personal investigation. But in *U. imber* it essentially agrees with what we found in the grebes.

A complete skeleton of *Urinator lumme* (No. 13,646 Smithsonian Collection) before me, has 43 vertebræ in its spinal column. Of these the *fourteenth* is the first to bear a pair of free ribs; the succeeding six movable vertebræ connect with the sternum by costal ribs; the next seventeen unite as a "sacrum" with the pelvic bones; then follow six free caudals and a pygostyle containing several more.

The dorsal ribs are broad, and bear large, freely articulated epipleural appendages. Two pairs of ribs also come off from the sacrum, and meet long, sweeping hæmapophyses, that reach the costal borders of the sternum. This specimen has also a "floating costal rib," which is very small and delicate. It is seen on both sides. The form of the skeleton of the thoracic parietes agrees to some extent with the shape it assumes in the Alcidæ, with its hinder ribs sweeping beneath the pelvis. This latter bone is of extraordinary form and dimensions in all of the Urinatoridæ, even excelling the grebes in some of its peculiarities. The anterior portion of an ilium is short and depressed in comparison with its extensive backward reach. The neural crest of the sacrum appears above the pelvic bones for its entire length, and posterior to the large elliptical ischiac foramen the ilium looks directly outwards, then outwards and upwards. A small prepubis is present, while the post-pubic element is long and slender, its posterior extremity, curving beneath the pelvis behind, is dilated and paddle-shaped. It nearly meets the fellow of the opposite side, where both are completed by an emargination of cartilage. It differs from the grebes in that it articulates with the postero-inferior angle of the ischium upon either side.

Five of the last caudal vertebræ, together with the pygostyle, are shown in side view in my above mentioned paper (*Jour. Anat. and Physiol*). The three first chevron bones there exhibited are freely articulated over the joints of the centra when they are present; the ultimate ones, however, become anchylosed to the under side of the rear vertebra in each case, the last one really forming the antero-inferior process of the pygostyle.

Coues in his examination of the skeleton in *Urinator imber*

found 13 vertebræ in the cervical portion of the spinal column, with nothing especially peculiar in their articulations,[1] and he says that although they "possess characters which most readily separate them from those of any other portion of the column, they yet differ greatly from each other, in different portions of the neck..... Beginning with the third vertebra, and proceeding backwards, we find that the length of the bodies increases successively to about the 8th or 9th, when it again decreases rapidly, so that the last one is not as long as the third. The body of the third is thin, being exceedingly compressed vertically; and coincidently with the lengthening of each one successively to the 8th or 9th, they grow wider, and comparatively not so deep vertically; those that follow, however, do not again grow more compressed as they shorten; but on the contrary become broader and broader, so that the last one is as wide as deep, and very stout and strong. With this widening, there is also, towards the posterior extremity of this portion of the spine, a very high development of the transverse processes of the anterior extremities of each vertebra. This is so considerable, that the width across these transverse processes much exceeds the length of the whole vertebra. These processes are also exceedingly stout, with several roughened eminences for muscular attachments; and the foramen for the vertebral artery, which their two roots form, is as large as the spinal canal itself. Now as we proceed up the neck to the head, these transverse processes project less and less from the bodies of the vertebræ, and become less robust and angular, at the same time that they are antero-posteriorly elongated; and possess regular lamelloid walls, so as to form rather canals than simple foramina for the artery."

"The 'styliform processes' or 'rudimentary ribs' appear to arise from the posterior aspects of the summits of each of the transverse processes, beginning with the third vertebra. They are directed backwards, exactly parallel with the axis of the

[1] Coues, E., The Osteology of the Colymbus torquatus, with notes on its Myology.— *Mem. Bost. Soc. Nat. Hist.*, i, pt. ii, Nov., 1866, pp. 131–172, fig. 2, pl. 5. This time-honored and excellent paper was also afterwards separately issued with a slight change in its title, but apparently without revision.

column, and, according to their length, form a more or less complete osseous covering and protection to the vertebral artery during its passage between any two contiguous foramina."

Then after describing the neural and hæmal spines of the "cervical vertebræ"; the axis and the atlas, Coues proceeds by saying that, "If we consider the *dorsal* as corresponding in number with the ribs, we should assign ten to this portion of the column. The last three ribs, however, correspond to vertebræ which are completely anchylosed to the sacrum as well as to the iliac bones, and at the same time they differ in several respects from the dorsal ribs proper. . . . ."

"The transverse processes of these [dorsal] vertebræ are as usual very broad, long, and thin; their posterior border concave, their anterior convex, and their postero-external angles prolonged backwards into a short 'styliform' process, more or less intimately connected with the next succeeding vertebra. The horizontal lamellæ of the transverse processes of the last four vertebræ are pierced by a quite large foramen."

"The superior spinous processes of the vertebræ are so long that they nearly touch each other by their anterior and posterior borders; only a slight space being left between them. They are quite regularly rectangular in shape, having straight, flat superior borders at right angles with the anterior and posterior borders. They are connected with each other by dense and strong ligaments, and probably become more or less completely anchylosed with age." He then carefully describes the *enormous* development of the hæmal spines of the dorsal vertebræ,—and although of much the same shape, the one for *U. lumme* (*Jour. Anat. and Physiol.*) gives but a feeble idea of their remarkable development in *Urinator imber*, the subject of the memoir from which I have been quoting. Among themselves the motion of the vertebræ during life in this dorsal region of the column is wonderfully restricted, and as I have shown above, in some grebes the dorsal vertebræ all fuse into one common piece.

Coues made out 15 vertebræ as being fused together in the pelvic sacrum; but in a specimen before me, after careful count, there appear to be sixteen. Marsh found but 14 in the sacrum of *Hesperornis regalis*.

From specimens at hand it would appear that in *Urinator lumme*, the ilia anchylose with the sacral vertebræ for the entire length of the sacrum, whereas in a specimen of *U. imber* before me (No. 18256, U. S. Nat. Mus.) fusion only exists opposite the acetabulæ and thence on anteriorly to the fore end, inclusive. In Hesperornis it was only opposite the acetabulæ that fusion took place.

As much alike as the pelves of *U. lumme* and *imber* are, there is still another interesting difference between them, for in the former the anterior ends of the ilia are seen to be quite obliquely truncated, — they are more or less rounded in the latter species. Marsh says of those bones in *Hesperornis regalis*, that "the anterior extremity of the ilium is thin, and rounded in outline" (*Odontornithes*, p. 69), but fundamentally the pelves of all these divers are much the same.

In describing the ribs in *Urinator imber*, Coues remarks (p. 144) that they "are ten in number. Of these nine articulate with the spine, and eight with the sternum. Seven only are dorsal ribs proper; the eighth and ninth being articulated with the sacral vertebræ posterior to the tip of the crista ilii, and the tenth being connected neither with the spine nor sternum. . . . ."

"As usual, the ribs consist of vertebral and sternal portions, movably articulated with each other. Both of these portions grow successively longer from before backwards; but the sternal portions much more rapidly than the vertebral. Thus while the sternal portion of the second rib is barely three fourths of an inch long, that of the seventh is fully three inches. The angle at the junction of these two portions, of course, varies with every stage of an inspiration and expiration; but at any given moment the angles become successively more acute from before backwards, — from the increasing length of the vertebral as well as the sternal portions. . . . ." The last rib differs from all the others in being unattached at either vertebral or sternal extremity. It consists merely of two extremely slender elastic bones, tapering to a fine point, somewhat larger and broader at their bases, where they are joined to each other. The sternal portion is longer than the vertebral. Close by the junction of the two, this sternal portion sends off from its posterior border

a small, slight process, which curves directly outwards and forwards, lying parallel with the posterior border of the rib, which it joins again about an inch from its origin, — leaving a space filled up only by membrane. This may very possibly be regarded as the rudiment of an eleventh rib, of which the vertebral portion is wholly wanting. It is sometimes entirely obsolete."

"The latter ribs project so far backwards, that the thoracic parietes are prolonged some distance behind the acetabula, and consequently the femur in its normal position lies directly over the last three or four ribs, and moves backwards and forwards upon them. The angle of the last rib reaches within less than two inches of the posterior extremity of the elongated obturator foramen" (*loc. cit.* pp. 145, 146).

Marsh says that "the ribs of *Hesperornis* present no marked features to distinguish them from those of modern birds. They are composed of dense bone, but some of them contain irregular cavities. The articulated vertebral ribs of *Hesperornis regalis* are nine in number, on each side. The first three of these were attached to the last three cervical vertebræ, and had their distal ends free. The remaining six are all well developed ribs, which were connected by means of the sternal ribs with the sternum" (*loc. cit.* p. 63).

In comparing Marsh's figures of the sterna of *Hesperornis regalis* and *Hesperornis crassipes*, I find upon either costal border of the sternum of the first-named species but *four* facets for articulation with the costal ribs, whereas in the latter form there are *five* represented; and from this I am led to believe that there was quite as much, if not more, variation in this matter of ribs among those now long extinct types as there is among their existing affines. (Compare Marsh's Plates vi and vii, Figs. 1, 2, and 1, 2 respectively.)

Grebes, loons, and the great toothed divers of the Cretaceous period all vary in this particular. And sometimes, too, as we know, they are apt not to agree even in the number of facettes on the costal border of the same sternum. Frequently the number varies for the genus Urinator now under consideration, of the family Urinatoridæ, — sometimes in the same species, but more often among different species.

A clavicle of the pectoral arch has a broad head, but is as thin as a knife-blade, the outer aspect of which, when articulated, simply rests against the summit of the coracoid, while its posterior end rides over the head of the scapula. This expanded part of the clavicle rapidly contracts in width as it descends, until it becomes quite rod-like, square on section, to curve abruptly towards the sternum, where it unites with the fellow of the opposite side to support in the median line rather a long, peg-like hypocleidium. Viewed from in front, the furcula is a wide U-shaped bone, with its lower arc curved more than usually upwards. In common with other bones of the arch, it is non-pneumatic.

The lower part of a coracoid is much expanded laterally, with smooth and evenly concave articular lower margin for the sternal groove. As in some of the auks, the lower lateral margin of the bone develops a prominent upturned laminated process. The shaft of the coracoid is transversely elliptical on section, and its scapular process may, or may not descend, upon its inner side, sufficiently far as to be pierced by the foramen, which likewise occurs in the Alcidæ. The head rears to a considerable extent above the glenoid cavity, and its tuberous summit curls over towards the median plane.

Larus glaucus possesses a coracoid that has the foramen in the scapular process, as well as the laminated externo-lateral apophysis as in Urinator, but its furcula resembles that bone as we find it in the auks and guillemots.

The scapula in the red-throated diver is short, and doubly truncate behind. Its curvature may be quite abrupt just beyond the head in some specimens. This latter is transversely narrow, and thickened from above, downwards; it occupies the entire upper margin of the scapular process of the coracoid.

In the Yellow-billed loon (*U. adamsii*), when the pectoral arch is articulated *in situ*, if the line of the long axis of the coracoid were produced downwards, it would cut the lower margin of the keel of the sternum at the junction of its middle and anterior thirds; the scapulæ are much tilted upwards, and the aborted hypocleidium of the furcula is over the tip of the carinal angle and separated from it by about a centimetre.

In *Urinator imber* the U is by no means as broad as it is in *U. lumme*, the upper expanded parts are even still thinner, and relatively somewhat larger, and finally, it totally lacks the hypocleidium. All this agrees with the os furcula of the loon, the skeleton of which Coues described (*loc. cit.* p. 148).

The coracoid of *U. imber* very closely agrees with that bone as we find it in *U. lumme*, but the foramen that pierces the scapular process in *imber*, is a constant feature in that species. The scapulæ of these two divers are essentially quite alike, except in point of size. A point to be noticed in this latter bone, is the fact that the head and neck is bent at a rounded angle, with greater or less abruptness with the continuity of the blade of the bone. This flexure (*U. lumme*, Spec. No. 13646 coll. U. S. Nat. Museum) is greater in one scapula than it is in the other; the angle being more acute upon the left side. It is very open in other specimens.

In *Hesperornis regalis* the clavicles in the adult did not fuse with each other at the middle point below, simply articulating at the point of contact. This is the condition of those bones in the very young of *Urinator imber*, an embryonic condition, as it were, that persists throughout life in the great extinct ancestor of our loon.

Comparatively speaking, in all the loons, we find the sternum to be a very large bone. It is twice as long as it is broad, and it has great triangular costal processes. An extensive oval notch on either side of the keel behind gives rise to lateral xiphoidal processes, while the mid-portion, shaped like a shield or an escutcheon, extends considerably more posteriorly, and does not entirely ossify around its hinder border until late in life. It may be pierced by a few foramina, where ossification has not been quite thorough. This part of the sternum is unkeeled, the keel at the best being very low, but with prominent and projecting carinal angle in front.

As I have said above, the usual number of facets upon either costal border is eight; there may, however, be but seven. The manubrium is broadly wedge-shaped and nearly aborted; its triangular, anterior face is slightly concaved. Costal grooves are long and deep, but relatively, not as deep as they are in the

grebes. They almost meet each other in the middle line, the interval between them being less than the width of manubrial base. On its thoracic aspect the bone is concaved, being most so anteriorly, and gradually shallowing as we approach its hinder part. Both this surface and the ventral one are very smooth. Upon the latter the 'pectoral muscular line' extends from the mid point of the lower lip of the outer third of the costal groove obliquely to the carina meeting it at the juncture of its anterior and middle thirds. In *U. imber* the bone averages 20 centimetres for its greatest length, and 8.5 cms. for its greatest breadth; — the last measurement being taken across the lateral xiphoidal processes. Though very light and elegantly proportioned the base is absolutely non-pneumatic throughout the superfamily. Its form is well shown in the sternum of *Urinator lumme* (Spec. No. 16628 of the U. S. Nat. Mus. Coll. ♀) but its pattern may vary considerably, being remarkably narrow and long in some individuals. When thus fashioned it reminds one very much of the sternum in certain of the auks. But among some water birds skeletal characters crop out very strangely sometimes, and even to the casual observer the sternum of an albatross, a cormorant, Plotus, a fulmar, and a grebe all more or less closely resemble each other upon a direct pectoral view, and to a less extent in several of those forms, when viewed from the side.

In concluding his account of the sternum of the loon, Coues says: "Viewing, now, the sternum as a whole, we have to notice how great an extent of surface is secured with a trifling increase of weight. Posteriorly, this is attained by means of the great lateral projection of the apophyses, as well as by their length, and by the breadth and projection backwards of the thin, almost cartilaginous xiphoid. Anteriorly, where the sternum is not so wide, the deficiency is atoned for by the great depth of the keel, and its projection forward; at the same time the outline of the crest of the keel is such that when the inequalities of the bone is all filled up with muscular tissue the resulting surface becomes flat, and broad as well as long, affording the best possible outline for contact with the water." (*loc. cit.* pp. 147, 148.)

According to Marsh "The sternum in *Hesperornis* somewhat

resembles in general form the corresponding bone in the genus *Uria*, but in other respects is more like that in the *Ratitæ*. It is thin and weak, and entirely without a keel. It is expanded in front, especially between the costal processes, and has two deep grooves for the reception of the coracoids. These grooves are placed obliquely, converging anteriorly, and are widely separated from each other. The sternum has a rounded mesial projection in front, which is somewhat thickened, but there is no true manubrium." .... "The sides of the sternum in *Hesperornis* are concave in outline, and in *Hesperornis regalis*, there are four articular projections on each side for the attachment of sternal ribs. These processes are all on the anterior half of the sternum. Behind these the lateral margins are nearly parallel. The posterior end of the sternum is quite thin, and had two shallow emarginations. In *Hesperornis crassipes* the sternum had five articular faces on each side for the sternal ribs. The posterior margin in the same species is less excavated than in *Hesperornis regalis*." (*Ordontornithes*. p. 60.)

If you will refer to Plate VII of Marsh's work, from which I have just been quoting, and examine Fig. 3 of the sternum of *Hesperornis crassipes*, it will not be difficult to believe that perhaps the sternum of that species had lateral xiphoidal processes something like those found in *Colymbus cristatus*. In the specimen they look very much as though they had been broken off, an accident very likely to occur in the sternum of a fossil bird, and frequently seen even in the sterna of our existing birds in the collections in the museums. The xiphoidal part of the sternum was cleft by a shallow triangular notch, in *Hesperornis crassipes*, precisely as we find it now in many of our existing grebes.

The Pectoral Limb in the Urinatoridæ.

All the bones of the upper extremity are non-pneumatic in this family. They are heavy, and when simply cleaned in the rough, they soon become dark and the oily substances contained in their cavities ooze out upon their outer surface in no inconsiderable amount.

The palmar aspect of the proximal end of the humerus has a large subcircular elevation upon it that is quite characteristic. This projects in such a manner that upon the reverse side it is seen extending beyond the border of the bone, near the shallow, pseudo-pneumatic fossa.

The radial crest from its size and length is more than usually conspicuous; its free border is a long convexity, and this plate-like process is carried well down the shaft, occupying fully one-third of its length. Below it, the shaft for its middle third becomes subcylindrical, showing a large nutrient foramen upon its ulnar aspect.

The distal end of the bone is not spread much in a transverse direction, but otherwise rather bulky. Two wide and shallow furrows mark it on the anconal side for the passage of tendons, and a large oblique and ulnar trochlea stand out upon the other. The ectocondyloid process is barely noticeable.

The radius is straight, and the major part of its shaft nearly cylindrical; its articular ends present the characters of the bone as seen in the majority of the class. When articulated, these alone meet the ulna, giving rise to a long, narrow, interosseous space. Towards this the larger bone of the antibrachium presents a concave border of a moderate degree of curvature. Its shaft, too, is quite cylindrical, and faintly shows the row of papillæ for the quills of the secondaries. It develops in a transverse direction not an inconsiderable ledge at its distal end, upon which the expanded end of the radius rests in articulation.

The carpus is composed of the two elements found in most birds; they are here simply somewhat modified in form for the family, and to accommodate themselves to the shape of the other bones with which they come in contact. They in turn having their own specific cast.

One of the first things that forces itself upon our attention in examining the skeleton of the hand of one of these divers is the unusual length (comparatively speaking) of the metacarpals. Of these, the one for the pollex digit is of an extraordinary length; much more than a third the length of the index one, and co-ossified with it in the usual manner.

I do not recall an instance among birds where the comparative

lengths of these two metacarpals is anything like it. The proximal phalanx of the pollex is also long and compressed. It bears a claw upon its extremity. Both of the other metacarpals are long and very straight, allowing but a narrow interval to exist between them.

The blade of the proximal phalanx of the index is meagre, being flat anconad and faintly pitted upon the opposite side. Its distal joint also bears a claw.

The phalanx of the middle finger is fully half as long as the expanded one of index alongside of which it lies.

These observations upon the pectoral limit of the Urinatoridæ have been jotted down during my examination of this part of the skeleton in a specimen of *U. lumme*, and in it I find the skeleton of the manus, just described, equalling in length the bones of the antibrachium.

The humerus in this diver has a length of about 14.5 cm.; the radius 11.4; the ulna 11.65; manus 11.8, of which latter the carpo-metacarpus claims 7.5 cm. From this it is seen that when the skeleton of the limb is in a position of rest and closed alongside the chest, the humerus projects beyond the bones of the anti-brachium for some little distance. This is not the case among the Laridæ, whereas it agrees with *Alca torda*, Uria, and, I expect, the Alcidæ generally.

The Pelvic Limb in the Urinatoridæ.

The skeleton of the pelvic limb in the Urinatoridæ is a very interesting structure, and highly characteristic of the family.

Coues has described its mechanism and structure in *U. imber* in his memoir before alluded to, and I will here record a few observations that I have made upon this limb as found in *Urinator lumme.*

The femur is short and thick, being about as long as the cnemial process of the tibio-tarsus above the articulation. Its short shaft is somewhat cylindrical near the middle, bowed to the front, and scarred in many places by tuberous projections for muscular insertion. The head is large and globular, sessile, and deeply marked by the pit for the ligamentum teres. Dis-

tally, it is much expanded in a transverse direction, the inner condyle being small and elevated, the outer one being very large, strongly cleft behind for the fibular head, much the lower of the two, and separated from its companion in front by a deep rotular fossa.

The patella of the red-throated diver and other loons is generally considered to be the flake-like bone articulating at the posterior base of the cnemial process of the tibia. Its form and exact position I have given in my paper on the patellæ in birds referred to in the second paragraph of the present paper. This illustration also presents the outer aspect of the femur, tibio-tarsus, and fibula; the latter two for their proximal two-thirds only.

Nothing could be more interesting than the form assumed by the tibio-tarsus of this diver. Its cnemial process is enormously produced, having a deep, longitudinal concavity between its pro- and ecto-cnemial ridges in front, and the two sides meeting in a median ridge behind. The pro-cnemial ridge is carried down as a wing for some distance on the side of the shaft. This latter is somewhat flattened from before backwards for its entire length, but better marked in this particular at its distal extremity, just before we arrive at the condyles, where also it is marked by the broad, shallow tendinal groove. This is bridged over by the usual bony span for the deep extensors.

The condyles are very prominent in front, but approach each other as low, sharp ridges behind. Coues found the fibula in the loon, "for an inch or so, quite separate from the tibia; is then united with it for some distance, becomes again distinct for about an inch, and then finally merges as a slender spiculum into the side of the tibia, rather more than an inch above the joint. A slight crest, however, gives an indication of it, which can be traced quite to the external malleolus of the tibia." This description agrees with one of the specimens of *U. lumme*, but in another it is carried down distinct and prominent to terminate in a well-formed malleolus upon the lower antero-lateral aspect of the shaft. The lower portion is anchylosed with the tibio-tarsus, but could, with but little difficulty, be separated from it with a good sharp knife. In other words we find specimens of *Urinator lumme* wherein the fibula is complete.

Four figures of the Plate illustrating the present paper are devoted to the extraordinary tarso-metatarsus of the Urinatoridæ as seen in *U. lumme*. These give various aspects of the bone, and distinctly show all the characters it possesses. Chief among these is the great amount of lateral compression of the shaft and trochlear end. The former is grooved both in front and behind for its entire length, forming a guide as well as a harbor for the passage of tendons.

The hypotarsus is very large, it being composed of a posterior arcade of bone with three distinct foramina piercing its substance in front of it. Occupying a position above the base of the mid-trochlea, the inner one of these three compressed protuberances projects the most posteriorly. The remaining two are separated by a cleft, which is continued above by a groove on the anterior surface, to be pierced obliquely from above, downwards, by the usual arterial foramen. The mid-trochlea is the lowest of all three, and rather the most anterior. They are all strongly marked by median grooves intended for the corresponding surface on each proximal phalanx of the digits.

A scale-like first metatarsal is suspended by a ligament attached to its entire anterior free border, to the inner inferior posterior margin of the shaft of the bone. It supports a feebly developed phalanx and claw representing the hallux digit. As for the three anterior toes, they are composed upon the usual formula for the number of joints as found in this member in the majority of the class. All of the ungual phalanges are in this diver flat and scale-like.

The proportionate lengths of these joints in the skeleton of the pes are shown in the following measurements: — Hallux joint has a length of but 1.1 centimeters, its claw but 0.5; the proximal phalanx of the inside toe measures 4.0 centimeters, the next joint 2.1, and its claw 0.95. The proximal joint of the middle toe 3.6, next joint 2.0, next 1.8, the claw 0.9; finally the proximal joint of the outside toe 2.8, next 1.6, next 1.4, next 1.8, and the claw 0.85.

Aside from the osteology and other interesting points of structure in the pelvic limb of red-throated diver, a notable feature is to be noticed in the great number of fibrous loops

attached to the long bones at a number of points, which serve to surround and guide the various tendons on their passage to the toes and prevent them from slipping from their places as they pass these narrow bones, when the limb is brought into vigorous action.

D'Arcy Thompson in his very excellent memoir "On the Systematic Position of Hesperornis" in contrasting the characters presented in the pelvic limb of *H. regalis* with the corresponding ones as found in the hind limb of *U. imber* says of the former that "Firstly, the extreme shortness of the femur is a very Colymbine feature; that bone is in *Colymbus* [*Urinator*] and *Hesperornis* about one-quarter the length of the ilium; whereas in the Ratites, except in exceptional cases, such as *Dinornis elephantopus*, the two bones are nearly of equal length. Secondly, and of greater importance, the patella, which, small and double in the Ostrich, is rudimentary or absent altogether in the other Ratites, is of immense size and peculiar shape in *Hesperornis*. In this bird it is a long trihedral pyramid, pointed at its superior extremity, concave on its outer surface, bearing at its lower extremity special and separate articular surfaces for the tibia and femur, and lying in a line with the long axis of the femur. Except that it is perforated for the tendon of the *ambiens* muscle (as in the Gannet), it is extremely like the patella of the Grebe, and practically identical with that of *Colymbus* [*Urinator*], except that in this latter it is fused with the upper extremity of the tibia. The existence of a small additional sesamoid in the knee-joint of *Colymbus* [Urinator] (Owen, *Comp. Anat. II.*, p. 83) does not invalidate the homology here adopted of the long 'rotular process of the tibia' with the patella." (pp. 11, 12.)

If Thompson means by this that in the loons (Urinator) the patella originally was separate as it now is in the grebes and held the same relative position to an elongated rotular process of the tibio-tarsus, as in the latter birds, and that since, in the loons, such a patella has come to be fused with the aforesaid process of the tibio-tarsus, the present writer is inclined to agree with him, although he formerly held the opinion that the small flake-like bone described by Owen was the only patella possessed

by the Urinatoridæ. Further along I shall refer to this matter again.

The study of the patella in birds is a very interesting, not to say, an important one, and, as has been noted above, as long ago as 1884 the writer published an article in the *Proceedings of the United States National Museum* on the subject (Vol. VII, pp. 324–331) in which was figured the patellæ of certain penguins, mergansers, gannets, grebes, divers, fulmars, Hesperornis, crows and cormorants; and to that article the reader is referred for information touching what has just been said above.

There can be no question about the existence of the patella in the grebes, nor in Hesperornis, nor in the cormorants, but as I have already shown, morphologists are not thoroughly agreed upon the nature of the flake-like sesamoid found at the knee in a loon, nor homologically speaking, its significance. Granted that a large patella in the Urinatoridæ has fused with the long cnemial process of the tibio-tarsus, then it would hardly appear that the small flake-like bone in the tendon of the extensor femoris muscle should be considered a patella at all, although in the matter of position it agrees with that sesamoid as it is found in all birds that possess it. It would hardly seem reasonable that Urinator had *two* patellæ at either knee-joint, and such very dissimilar ones. In my opinion the last word upon this subject remains yet to be said. The embryology of the Urinatoridæ, as well as the morphology of the structures involved in specimens of nestlings and subadults of the species in all stages of their growth, requires investigating.

In the *Journal of Anatomy* (London) (Vol. XXIV, January, 1890, and other volumes) I published a "Brief Summary of the Principal Osteological Characters of the Urinatoridæ" to which I refer the reader for further details regarding the osteology of the grebes and loons.

It now remains for me to compare the principal osteological characters of the loons and the grebes. These may be conveniently arranged for reference in the following manner:—

A few of the Osteological Characters which distinguished the Podicipoidea and the Urinatoroidea.

Podicipoidea.— Pars plana ossifies.

Urinatoroidea.— Pars plana does not ossify.

Podicipoidea.— Supra-orbital glandular fossæ but faintly mark the skull.

Urinatoroidea.— Supra-orbital glandular fossæ deeply mark the skull, being within the superior border of the orbit and separated from each other mesially by a *thin*, longitudinal crest of bone.

Podicipoidea.— Twenty-four (24) or more dorso-cervical vertebræ.

Urinatoroidea.—Twenty (20) dorso-cervical vertebræ. Not more.

Podicipoidea.— Sternum *short* and broad, with the lateral xiphoidal processes extending more posteriorly than the mid-xiphoidal piece, which latter is triangularly notched in the middle line.

Urinatoroidea.— Sternum nearly twice as long as it is broad, with the lateral xiphoidal processes not extending more posteriorly than the mid-xiphoidal piece, which latter is unnotched and rounded off posteriorly.

Podicipoidea.— Posterior free extremities of *os furcula* very narrow and pointed.

Urinatoroidea.— Posterior free extremities of *os furcula* very broad, laterally compressed, and apices bluntly rounded off.

Podicipoidea.— Posteriorly the ischium does not articulate with the superior margin of the very long post-pubic style, anterior to its free end; and the latter is not perceptibly dilated.

Urinatoroidea. — Posteriorly the ischium does articulate with the superior margin of the very long post-pubic style, anterior to its free end; and the latter is considerably dilated and paddle-shaped.

Podicipoidea. — Pollex metacarpal short.

Urinatoroidea. — Pollex metacarpal remarkably long.

Podicipoidea. — Possessed of a large patella, co-existing with an elongated cnemial process of the tibio-tarsus.

Urinatoroidea. — Possessed only of a very small, flake-like sesamoid, which occurs in the tendon of the extensor femoris muscle at its insertion; and probably the true patella has coössified in the adult with the elongated cnemial process of the tibio-tarsus.

Affinities of the Pygopodes.

Taken in connection with many other good characters presented in the structure of grebes and loons, we must believe that the differentiating osteological ones just given above, point to the fact that the relationship now existing between these two well-defined groups of birds can best be appreciated by creating for them a superfamily in each case. To this end I consider the grebes to compose the superfamily Podicipoidea, and the loons the superfamily Urinatoroidea.

In 1884 (*Proc. U. S. Nat. Mus.*, vol. vii, p. 331) I considered the representatives of the extinct genus of cretaceous toothed birds, Hesperornis to be "powerful divers" and the "ancient ancestors" of our present existing grebes and loons.. Essentially, this still remains my opinion; and, at a later day, after carefully comparing the osteological characters of the Podicipoidea and Urinatoroidea with the corresponding ones in the skeleton of *Hesperornis regalis* and *H. crassipes* as given by Marsh, I again said that the result of those investigations "convince me of the fact that, however widely separated now, our existing loons and grebes are derived from the same ancestral stock to which *H. regalis* belonged" (*Jour. of Anat.* London, Jan., 1890, p. 169).

Our existing grebes and loons then are derived from, or are the descendants of great toothed divers long since extinct. Possibly the Hesperornithidæ were an offshoot family of a superfamily,— the Hesperornithoidea, the latter the more typical of these extinct divers, and from them our present Pygopodes were derived, but we yet lack the necessary material to place such a question beyond dispute. From a consideration of the osteolog-

ical characters I consider the Podicipoidea to be an earlier offshoot of the pygopodine stem than the Urinatoroidea, and more nearly related to Hesperornis than are the latter birds. The morphology of the pelvis and the pelvic limb, as well as certain characters in the skull and trunk skeleton, point, I think, in favor of this view.

No doubt but what the Hesperornithidæ were in their turn derived from still more ancient ancestors possessed of the power of flight, and in the ages to come our present-day Pygopodes, if it be their fate to have descendants, direct or indirect, those descendants may in turn again become flightless forms through a gradual loss of their pectoral limbs.

So far as the affinities of the Pygopodes are concerned with other groups of existing birds, we shall see in other memoirs I propose to publish on the subject that they present a number of osteological characters exhibited in common with the Alcæ and the Longipennes.

EXPLANATION OF THE PLATE.

(Limb-bones of Water Birds: all drawn by the author, about five-sixths natural size.)

Fig. 1. Right femur of *Urinator lumme*; anterior surface.

Fig. 2. Right femur of *Urinator lumme*; inner surface.

Fig. 3. Right tarso-metatarsus of *Larus delawarensis*; anterior aspect.

Fig. 4. Right tarso-metatarsus of *Larus delawarensis*; distal extremity viewed from below.

Fig. 5. Right tarso-metatarsus of *Larus delawarensis*; proximal extremity viewed directly from above; nat. size. Figs. 3, 4, and 5, all from the same specimen.

Fig. 6. Right tarso-metatarsus of *Hæmatopus bachmani*; anterior aspect.

Fig. 7. Direct view from below, distal extremity, same bone as in Fig. 6.

Fig. 8. Direct view from above, proximal extremity of the right tarso-metatarsus of *H. bachmani*, same bone as shown in Figs. 6 and 7.

Fig. 9. The same bone as in last figure seen upon the inner aspect of its distal extremity. (All from specimen 13636, coll. U. S. Nat. Mus.)

Fig. 10. Right tarso-metatarsus of *Chiornis minor*, anterior aspect. (From Dr. Kidder's type specimen.)

Fig. 11. Direct view from above, proximal extremity, same bone as in last figure.

Fig. 12. Direct view from below of the distal extremity of the right tarso-metatarsus of *Chiornis minor*.

Fig. 13. Right femur of *Chiornis minor*; anterior surface.

Fig. 14. Right femur of *Hæmatopus backmani*; anterior surface. (No. 13636, coll. U. S. Nat. Mus.)

Fig. 15. Right femur of *Larus delawarensis*; anterior surface.

Fig. 16. Right tarso-metatarsus of *Urinator lumme*; inner surface.

Fig. 17. Right tarso-metatarsus of *Urinator lumme*; anterior surface. Same specimen.

Fig. 18. Direct view from above, proximal extremity, of the same bone (*U. lumme*).

Fig. 19. Right femur of *Urinator lumme*; posterior surface.

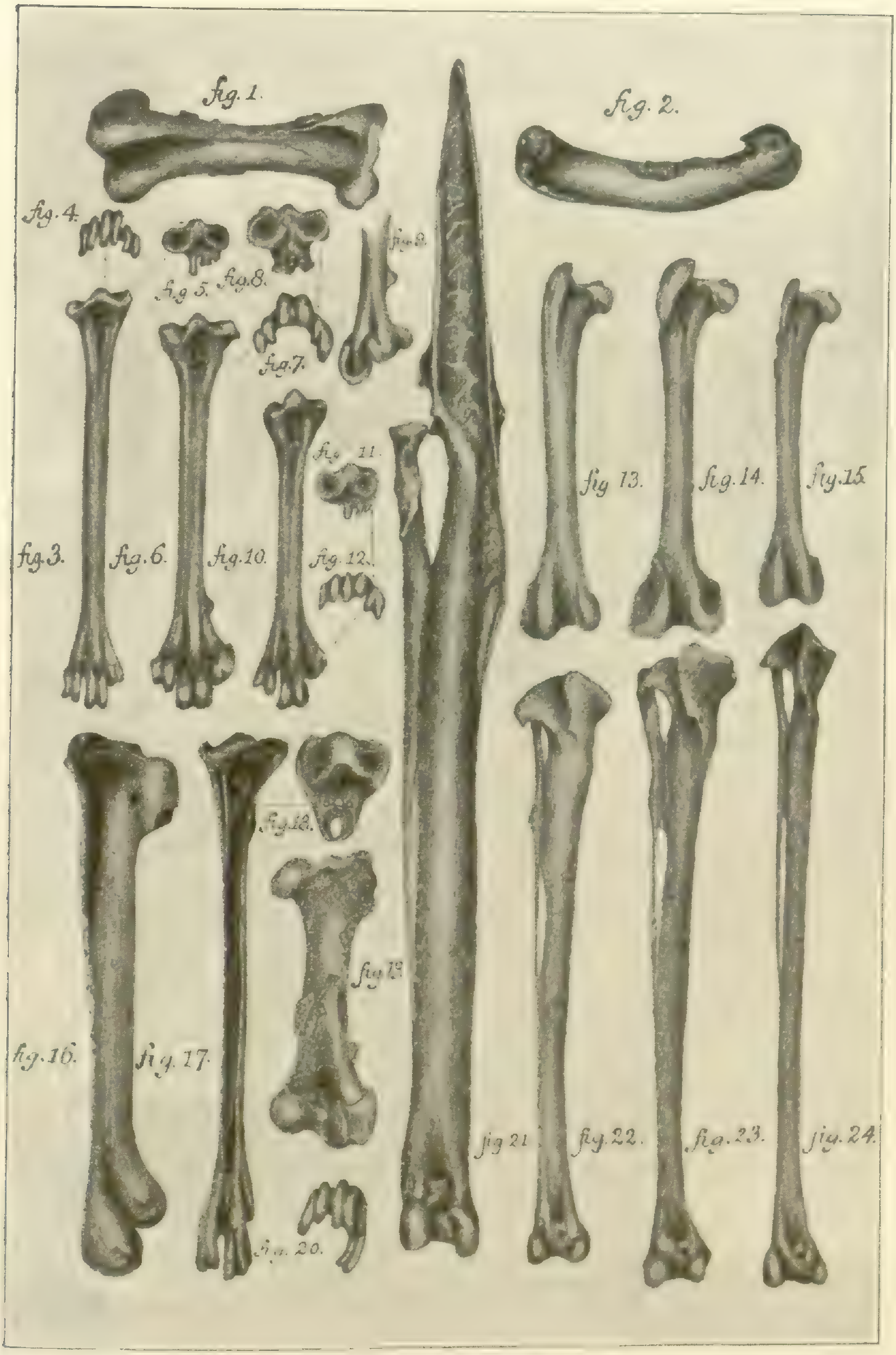
Fig. 20. Direct view from below of the right tarso-metatarsus of *Urinator lumme*, distal extremity.

Fig. 21. Right tibio-tarsus and fibula of *Urinator lumme*; anterior aspect.

Fig. 22. Right tibio-tarsus of *Chiornis minor*.

Fig. 23. Right tibio-tarsus and fibula of *Hæmatopus backmani*; anterior surface. (No. 13636, Coll. U. S. Nat. Mus.)

Fig. 24. Right tibio-tarsus and fibula of *Larus delawarensis*; anterior surface. From the same skeleton that furnished bones for the other figures given above.



Mo. Bot. Garden
1903

THE ERUPTION OF MOUNT PELÉE, 1851.[1]

TRANSLATED FROM THE FRENCH OF LEPRIEUR, PEYRAUD AND RUFZ BY

T. A. JAGGAR, JR.

TRANSLATOR'S NOTE.

THE following account of the eruption of 1851 is a valuable geographical record for students of the recent volcanic happenings in Martinique, and the only printed copy of the original report known to the writer is in the library at Fort de France. The region described as the seat of activity in 1851, a gorge adjacent to that containing the Etang Sec, is practically identical with the site of the crater of 1902, or parts of it, and the very careful description of earlier conditions there throws light on many of the phenomena of the later eruptions.

The investigating commission of 1851 report (1) abundant *pumice* in the old rocks of the mountain, (2) no activity at the summit lake, (3) unusual amount of water in the Etang Sec, (4) entire absence of lava or incandescent material, (5) fragments of diorite ejected, (6) hot waters, steam and dry rock-dust from the vents, (7) a local tornado, (8) sulphuretted hydrogen, (9) a buzzing noise or intermittent detonations. In a very suggestive footnote they comment on the superficial quality of the explosions, and although not themselves geologists, they conclude that Mount Pelée has never ejected molten lava in any considerable amount, but has always belonged rather to the cinder-cone type of volcanoes. There are, in fact, some ancient lava flows and intrusive sheets, but they are rare, the tuffs and agglomerates everywhere predominating.

No attempt has been made to eliminate errors in the original account. There are some geological and chemical phrases that are

[1] Official Report of 1851.— The manuscript was apparently drafted by Dr. Rufz. The translator obtained access to the printed copy of this report, kept in the library at Fort de France. Eruption du Volcan de la Montagne-Pelée. Pub. in 1851. E. Ruella & Ch. Arnand. Imprimeurs du Government, Rue du Bord de Mer, 94. République Française.

antiquated and obviously inaccurate. The same is true of the opening sentence — there is certainly good historic evidence of the activity of Pelée before 1851. The notation for magnetic directions is obscure, and in such cases the original symbols are reproduced in the footnote. Making due allowance for trifling inaccuracies, the report as a whole is the most complete and scientific record extant of the topographic details of the southern slope of Pelée prior to the eruptions of 1902–03.

October, 1903.

THE OFFICIAL REPORT, 1851.

A tradition without historical foundation records Mt. Pelée to be a volcano. The conical form, the crater lake, the pumiceous soil, all fostered this supposition. It was known also that in one of the gorges there was sulphur, and the inhabitants living near called this the Soufrière. The druggist Peyraud made a scientific excursion there in 1838[1] and brought back stalactites of pure sulphur attached to the leaves of a tree.

[1] Letter to the "Directeur de l'intérieur," by Peyraud: —
Monsieur le Directeur général.

Jài l'honneur de vous addresser un petit flacon contenant de l'eau que j'ai rapportée de la source minérale qui se trouve sur les terres de M. Huc, à la naissance de la Rivière Claire. Je dois vous observer que cette eau que l'on màvait dit être à 60° Reaumur, nèst dans ce moment qu'à 16°, et l'air ambiant à 18°. J'y joins un échantillon de la matière jaune qui tapisse les bords du morne d'ou cette eau découle, puis un morceau de bois recouvert d'un mousse qui répand une forte odeur de marée. Ce bois a été recueilli à quelques pieds au-dessus de la source minérale, un peu à gauche en faisant face à la montagne. Je vais m'occuper de l'analyse de cette eau et m'empresserai de vous eu faire connaître le résultat.

Pour vous donner une idée de la quantité de gaz hydrogène sulfuré qui se dégage dans les environs de la source, je vous envoie un porte-crayon en argent que je portais sur moi lors de mon excursion. Il est à regretter que la nature ait placé cette eau dans un endroit ne permettant pas d'y former un établissement qui aurait été bien avantageux pour la colonie. Plus tard je ferai en sorte de vous addresser le plan de l'endroit òu se trouve la source. Si vous désirez une plus grande quantité d'eau je me ferai un vrai plaisir de vous en faire puiser, que je renfermerai dans les flacons à l'émeri afin d'éviter la perte du gaz.

Je compte aller, dans quelques jours, parcourir la route de la Trinité afin de visiter l'endroit qui répand une odeur sulfureuse et vous rendrai compte immédiatement du résultat de mes recherches.

Je suis avec respect, Monsieur le Directeur général.

Votre tres humble serviteur,

Saint Pierre, le 20 Mai, 1838.

P. PEYRAUD.

Recently the inhabitants of the Prêcheur heights have complained of a strong sulphurous odor. Some of them have visited the Soufrière and report a fuming hole which has appeared, the vapors mixing with the clouds and thus being imperceptible to sight at a distance. On the 3rd of August the patrolman Carbonel brought in a partridge found dead near the new opening, and he said there were many others, that all the birds dropped dead when they flew over the fatal cavity. Like the Avernus of the Ancients,

> Quam super haud ullæ potevant impune volantes
> Tendere eter pennis: Talis sese halitus atris
> Faucibus effundeus supera ad convexa ferebat;
> Unde locum Graii dixerunt nomine Avernon.
>
> *Virgil.*

This year (1851) from the 10th of May, there were no earthquakes in Martinique, but Guadeloupe had many of them and was in continual fear. August 5, St. Pierre was peaceful; the weather had been fine. Towards 11 p. m. a dull, distant sinister noise began, like thunder; it was mistaken for thunder, or for the roar of the river in flood. The noise increased, waked many people and caused alarm.

I was in my villa of Fonds Canonville, very near the source of the sounds. I thought it was thunder, but was astonished at its continuance; I heard the workmen call me from without. They shouted "Do you not hear that noise?" I answered, "Yes, it is thunder!" "No, it is the Soufrière." I rose and looked towards Mt. Pelée, but could see nothing: the noise continued. The rest of the night was passed in great anxiety, and torches were seen indicating the flight of many people. No one knew anything definite and the answer to all questions was, "C'est la Soufrière qui bout!"

St. Pierre was equally frightened. In the morning roofs, pavements, leaves of trees, all were covered by a thin layer of grayish cinders, which made the town look like a European city covered by the white frost of the early days of autumn.

These ashes covered the country between the city and Mt. Pelée, covered Morne Rouge, and extended to Carbet. The

stream called the Rivière Blanche, because of the color of its water (caused, like the "yellow baths" of Guadeloupe, probably, by the presence of an iron hydrate) became black, charged with ashes or mud, and this coloration of the water could be seen far out to sea, as in time of flood.

The spirit of the city was an anxious curiosity, dissimulating, according to the light-hearted spirit of the country, under many jests. A few brave spirits made a reconnaissance of the mountain, and from their description the first accounts were published in the "Courrier de la Martinique" and in "Les Antilles."

The government appointed an investigating commission; Le Prieur, chief Pharmacist of the colonial hospitals, who had already made several explorations in Guiana: Dr. Rufz, and pharmacist Peyraud. The present document is the report of this commission.

The general aspect of La Montagne Pelée, seen from St. Pierre, is that of a great cone, from whose summit descend sharp spurs down to its base, these spurs being separated by an equal number of gorges or valleys. It resembles the cone formed by a pleated filter paper. In order to reach the summit of the mountain it is necessary to follow one of the spurs, for the valleys are often precipitous gorges. On August 28, we took what is considered the most direct route, by way of the sugar plantation "Rivière Blanche," near the farm Paviot, and came out at the habitation Ruffin. Ruffin is a farm 1½ hours horseback from St. Pierre, 551 meters above the sea. We slept there: 7 a. m. the morning of Aug. 29, the thermometer marked in air 23° Centigrade and 22.5° in the earth. At St. Pierre at this hour, 27° or 28°. We descended by a zigzag path to the bottom of the ravine of the Riviere Claire. This path is cut in "*pumites*," or local pumice stones which are white and friable, in little fragments. The Rivière Claire is so-called by way of contrast to the Rivière Blanche. The latter, whose waters are always milky, comes from one of the creases in the mountain separated from the Rivière Claire by a steep spur: both flow separately above, but unite below, and continue to the sea under the name of the Rivière Blanche. It appears that now the Rivière Claire receives the volcanic mud and blackens the

Rivière Blanche, no longer deserving its name of "clear." At the bottom of the ravine where we were, the Rivière Claire forms a cascade 2 or 3 meters high: it is only a brook that one can easily jump over. Its banks were covered with from 15 to 20 centimeters of mud. The water has ceased to be drinkable.

After having crossed the bed of the Rivière Claire, it became necessary to climb the opposite slope which is a very abrupt escarpment, where the first explorers had to construct a path, by means of a ladder of ropes and lianas: for a half-hour one goes upstairs in this fashion. The slope becomes easier and we are in virgin forest. There is no path. In order to advance in the direction of the hill one must push through palms, and tree-ferns, the long spines of which make treacherous support. This is the forest zone called the "little woods" in the colonies as opposed to the "great woods" where there are great trees remarkable for their height and the size of their trunks. About ten o'clock we reached the point where the first traces of the eruption were visible. The foliage of the ferns, bananas and other plants which form the vegetation of these places was dried and reddened as if it had been burned; on the leaves and on the soil also there was a thin layer of dried mud, the remains of volcanic ejections. Here the barometer registered a height of 846 meters. From there on the volcanic mud became more and more abundant. It covers the leaves in a dry adherent mass, and on the ground it is viscous and sticky and appears like a gray clay, in some places more than a foot thick: little scintillating points may be distinguished on the surface which the lens, and later a chemical analysis, showed to be globules of iron sulphide. As we had noticed that the leaves, branches and trunks of trees were plastered with mud only on the side toward the volcano, we thought at first that the weight of the mud was sufficient to explain the inclination of all these objects; they seemed to be depressed violently, but the quantity of mud on the leaves was only a few millimeters thick and not sufficient to break the branches; we soon saw that something more than the weight of mud must be called in to account for the disorder, and a sort of chaos through which it soon became necessary to thread our way. Here were great trees broken, overturned,

twisted, not only in one direction but in all directions, and often in a direction the reverse of that affected by the weight of the mud. This brought to us the conviction that something like an explosion had taken place. The air, displaced first by hot vapors blown out of the volcano, and rushing into the vacuous places so formed, became involved in a whirl or local tornado: we say local for the signs of disturbance were only in the vicinity of the volcanic opening. The people who fled with torches from the houses lower down the slope did not have their flambeaux blown out by the wind.

Climbing higher, the mud layer became thicker making the walking difficult and woe betide those with light or ill-made shoes! At the same time the crest of the spur we were following became narrower; a moment arrived when we had on the east, on the right-hand side, the ravine of the Rivière Claire. It was this last we were following, guided by the vapors that were rising from this gorge. Beside it we walked on a high crest rising above the bottom of the valley 50 to 60 meters; at our feet the valley of the Rivière Claire was plainly visible. From this point we obtained a full view of the effects of the eruption of the 5th of August, in all its extent and horror. The verdure is absolutely gone from the place which was formerly the scene of densest foliage. Trees, leaves, flowers, all are buried as though under a gray shroud. It is the sadness of winter with the trees denuded and smutted with a black snow. Though we found no dead birds, we also heard none of them singing. The mountain whistler, whose sweet pipe is associated with the melancholy grandeur of our "grands bois," the whistler of our mountains has fled from these his former haunts; we did not even meet the deadly trigonocephalus whose home is here. A dread silence, a sky obscure by vapor, an atmosphere charged with a strong odor of sulphuretted hydrogen, complete this scene worthy of Tartarus. The slope of the bed of the ravine in the midst of all this desolation, is very steep; it extends from the east toward the west from the summit peak of Mount Pelée called "Morne LaCroix," but the bottom is not continuous; it is interrupted by several cliffs; here and there, in the midst of the general grayness rifts may be seen where the soil is rent

bare; these are crevasses made perhaps by the steam of the mountain or by earthquakes about the rent. Ancient pumices may be seen of various colors, reddish or grayish, and among these are some rare masses of gray dioritic rocks, or of porphyries that the ancient fires have hurled out of the entrails of the earth along with the pumice.

In the upper part of the valley there are rising dense sheaves of whitish smoke which mark two volcanic vents from which came the mud that covers the valley and its environment. At eleven o'clock we arrived at the level of these two craters, from which we were separated only by the valley itself. A barometer reading here gave an elevation of 966 meters above sea-level. The temperature of the air was $23^{\circ}.5$ at twenty-five minutes after eleven o'clock; after removing the mud, the temperature given by a thermometer buried in the soil was $21^{\circ}.5$; this was $\frac{3}{10}$ more than the heat found at the lower station, where the persisting vegetation protected the soil from the direct action of the sun's rays.

But this was not the upper limit of the action of the volcano. It was easy to see that mud had been thrown several hundred meters above the orifices, for the line of green verdure did not begin to appear except at the very summit of the mountain. We wished to reach the summit in order to see better the actual extent of the lands covered by erupted material, but our guides assured us that the ascent here was not possible, that we should be cut off by cliffs and that there was no path. Looking over the scene of desolation, we estimated that the action of the volcanic eruption took place within a perimeter of something more than eight or nine hundred meters.

It was necessary to go down to the bottom of the valley in order to explore and examine the orifices themselves; to do this we had to slide down, with the aid of roots and lianas, an abrupt cliff 15 or 20 meters high; the younger and more agile members of the party decided to do this under the leadership of Mr. Peyraud. As they approached the fuming vents ahead of them, they found the mud deeper; the valley was divided in two branches by a spur from the summit of the mountain. In the right hand branch are the two craters; they lie in a N-S line, separated by a space of 25 to 30 meters, in the midst of which

the waters which descend from the mountain have worn a channel 12 to 15 meters deep. At this time the vents were almost free from vapor — something hitherto unknown since the day of the eruption. Therefore it was possible to examine them thoroughly. The left hand vent opens in the right slope of the spur which divides the upper part of the valley; it is of irregular, circular form and three or four meters in diameter. From this opening the thick vapors are discharged with the greatest force; these appear brilliantly white in the sunlight, spreading to leeward in a billowy plume, but they are denser and blacker in the immediate vicinity of the orifice; the emission of vapor is not preceded by any subterranean noises. The detonating sounds heard take place at the instant the vapor escapes from the hole, and this leads us to the belief that this noise is the result of the expansion of steam in air, a phenomenon entirely comparable to the detonation of a cannon.

This opening is reached by a sort of open gallery about a meter and a half wide excavated in a reddish pumiceous rock covered with dark gray mud, which was unstable and so hot that it was impossible to hold it in the hands more than a few seconds, especially that on the immediate rim of the crater. Here the attempt was made to sound the depths of the cavern by means of a zinc pail attached to a cord. But when the cord was withdrawn the pail had disappeared without evidence as to whether the loss was due to insecure knots or the melting of solder. The cord was impregnated with a strong smell of sulphuretted hydrogen. Stones dropped into the hole were heard to fall quickly with a noise as of striking a liquid. An alcohol thermometer buried in the soil rose almost to its highest limit. The barometer gave an elevation of 883 meters, indicating that these rents were 83 meters below the summit of the spur, where the rest of us had remained.

This crater had already been visited by Mr. de Maynard but that was in the first days of its formation when steam action was so violent that details could not be seen.

Across the gulch, but separated as we have said by twenty-five or thirty meters, is the other higher orifice, and this is also the greatest vent,— it is harder to reach than the first, lying at

the bottom of a great four-sided funnel behind which is a very high cliff ; this funnel opens against the wall of the cliff like a great chimney. One of the guides at that point venturing a little too near slipped on the steep slope leading to the orifice and was almost thrown in, but happily he checked himself just in time and we were saved from a horrible tragedy.

It was noon, and the openings, which up to that time had been giving off very little vapor — so that no steam could be seen from St. Pierre — began to puff and give off an odor of sulphuretted hydrogen more strongly than heretofore, and at the same time detonations could be heard. We thought of returning, but we wished to visit a third crater seen fuming some hundreds of meters lower down the same ravine, which was said to be the seat of the ancient Soufrière.

Two routes appeared practicable : the one following down the steep crest that we had come up by, in order to find, a little lower down, a less steep slope ; the other going directly from the upper orifices to the one below following the same ravine longitudinally ; the first of these routes was, according to the guides, the only practicable one ; the other passing escarpments and cliffs led to an inaccessible point above the vent. Mr. LePrieur and I followed the guides, Mr. Peyraud and some others who were with us wished to try the more difficult route, but after much trouble, they were obliged to retrace their steps and rejoin us. They had been cut off by those precipices which on the mountain are invisible a very short distance away, but which prove when one reaches them that the straight line is not always the shortest road between two points.

After going down a half hour we arrived at the level of the third crater, but it then became necessary to drop down into the ravine for a depth of fifty feet by sliding on a slope inclined about thirty degrees. Finally we reached the bottom and found the bed of the ravine four or five meters wide, in the middle of which a swift brook runs through a bed of grayish mud. This mud has a thickness of half a meter. On the two banks rise wall cliffs eight to ten meters high. The bottom of this gorge is thus in a fashion shut in. To the east, above, in the direction of the higher vents that we had just left, the ravine is

shut off by a rock wall at the summit of which gushes out the steam of the third crater; along with the steam, a cascade of water escapes, which falls into the ravine and forms the brook mentioned. Unfortunately it was not possible to climb to the edge of this hole and get a good view of its dimensions. The cliff which rises above it at the back is hollowed out in a sort of cavern, and before it the crater forms a *v* shaped breach whence comes the water of the cascade; it is probable that the arrangement of these places changes from time to time under the different forces at work, for Mr. Peyraud who had been here in 1838, found the place unrecognizable in 1851. Besides the crater of to-day which was quite new to him, there was lacking a cold spring which our companion had promised us and which for several hours we had counted on for quenching our thirst. We found only springs of hot water, the coolest of them at 37°.

On the heights above the ravine, the Abbé Lespinasse, during the first days of the eruption, had planted a cross, in order to reassure the frightened populace. This is the only barrier that man dares oppose to threatening nature at such a time. The presence of hot water here appeared to us an important basis of more extensive study. On our right looking to the east, about a meter and a half from the bottom of the ravine and three meters from the rock wall which cuts it off, there is a hot spring having a temperature of 70°; its taste and its odor indicate the presence of sulphuretted hydrogen. The principal jet is about an inch in diameter and all about it are tiny rills at the same temperature: two meters above this first spring and a little further along there is a second spring of the same quality with a temperature of 46°, which falls, by several little cascades, on the rock, from which it rebounds below. The action of the air liberates a great part of the sulphur contained and this is deposited in a light powder on the lower rock, which is coated yellowish white, but in falling lower down on another ferruginous rock it is again decomposed and the sulphur this time combines with the iron to form a black sulphide of iron.

On the same side going higher another spring is found with a temperature of only 22°; this has a still more sulphurous taste. On the opposite bank two meters from the bottom and one

meter from the end cliff there is another sulphurous spring with a temperature of 90°. The muddy water coming down the brook has very variable temperature; during our exploration, Aug. 29, it was 37°, but on the 30th it was 65° (for the study of the springs about this third crater was found so interesting that Messrs. LePrieur and Peyraud returned twice to take the temperature and to get some bottles of water for analysis). It is to these gentlemen that we are indebted for detailed information concerning the springs; they determined that the temperature of the different springs coming out of the rock was always the same, while that of the main brook varied; this difference according to them is due to the fact that the materials thrown out of the crater mix with the water of the brook, the source of which is rainfall. This is properly the head-waters of the Rivière Claire. According as the ejectamenta are more or less abundant the water is more or less hot. This we had opportunity to prove Aug. 29th, for while we were in the ravine making observations, suddenly several detonations were heard and at the same time blacker and more abundant fumes came from the crater; the water of the brook changed quickly in temperature rising from 27° to 47°. There were twenty of us crowded together in the ravine. Nearly every one was afraid and each sought safety on the adjacent cliff a few meters high. But as this could be reached only by one very narrow path, in single file, the crowding added to our panic. To the credit of Messrs. LePrieur and Peyraud be it said they did not share our fright and remained behind facing the eruption and continuing their observations, and they did not rejoin us until a long time afterwards. At the moment of the noise and the ejection of vapor a cloud of grayish mud was thrown into the air which fell in a very fine powder on our hats and clothing. The brook increased in volume to a blackish gray boiling mass. It did not appear to ever reach a depth of more than one meter, for the mud-stains on the wall were not visible at any point above this height. After three successive explosions the crater became quiet and the vapor became whiter. It was at this time again determined that the noise took place entirely at the orifice of the vent by the expansion of steam in air, and was in no sense

subterranean, for the puff of vapor and the noise were exactly simultaneous. We saw no ejections of fire, stones, or even sand; the only accident that was somewhat remarkable was the detachment of a block of ferruginous rock from the right side of the ravine, which rolled into the depths and broke into pieces. This rock measured twelve to fifteen cubic meters. On the sixth of September, Messrs. LePrieur and Peyraud on their second return hither determined that in spite of the thick masses of vapor thrown out since the 29th of August, and in spite of rain which had fallen twice on the mountain, the level of the brook had not risen. They said that our foot-prints of the last excursion were still visible in the mud of the bottom of the ravine, some of them containing a little water, evidently from rain-fall: in the interval between the two visits there was no change, and the different springs showed the same temperature; in the spring at 70° one could boil eggs, and some of the native crawfish were found cooked.

A copper bucket was thrown into the crater securely attached to a cord; three times the vessel was thrown against the rock wall and was recovered dented, but it was not possible to obtain the slightest particle of liquid; the material of the interior was found to be reddish pumice which accounted for a reddish color that had been at one time observed in the vapor coming from this orifice. While we were there, however, this steam and that from the upper crater always appeared to us white or blackish, the last condition being due to particles of sulphurous mud.

In order to complete the exploration of the scene of eruption it remained to examine the valley where the first openings were made. For the openings that we have just described are not those which opened first. Those which are in action today opened on Saturday, the 9th of August, after a series of detonations more violent than those of the 5th. The first openings are situated in a lateral valley which joins the one where the active craters are, but much lower down. They are today entirely quiescent. From the calm which reigns in their vicinity one would never suppose that a month ago they had served to give vent to the first manifestations of a volcano. These openings are ten in number, along a single line, and trend in the

same direction as the upper vents; behind them is a high cliff which forms the right side of the ravine they occupy. The first is at the same time the lowest and smallest; its diameter is 0.60 meter to 0.70, and its depth about 0.30 m. The bottom is covered with a reddish ferruginous sand and the rocks thereabouts are brownish and tumbled in disorder, doubtless the product of the eruption. The ravine has been deeply excavated by water which has removed the greater part of the soil and left only denuded rocks. The different openings are on a rather steep slope. The tenth which is the highest of all is also the widest and deepest; it is four meters long and a meter and a half wide. Above there is a tree supported by its denuded roots; this vent is quite deep and appears to contain water still, but a line forty feet long failed to reach the bottom; the third opening, counting from below, is also of elongate shape; it is not remarkable except that it is half covered by a boulder which has not been displaced. There are also some plants which have not been totally destroyed and their roots hang denuded in the opening. The bottom of this cavity is, like that of the other, covered by sediment colored with iron oxides. An elevation taken at half past three in the afternoon in the middle of these small openings gave 816 meters above the sea. The thermometer gave 20.5° in the air and 23.5° in the soil; much rain fell on that day.

In returning to the habitation Ruffin and passing the Morne Plumet, — the most elevated point of this part of the mountain and hence named Gros Morne, — one does not encounter any trees, the only vegetation being shrubs, grasses and sedges; at this height (812 meters above the sea) there is a fine view; directly opposite is the ravine of the Claire within which are the three active openings, to the left extends all the district of Prêcheur with its picturesque farm houses situated each on its little hill, and to the right in the distance may be seen the wide landscape of St. Pierre, the city itself with its reddish roofs, and the vessels anchored in the roadstead.

The general direction of trend of the ravine where the active steaming vents are situated is ENE.[1] From the summit of the

[1] The French notation used is N. E. 1/4 SE.— W. 1/4 W. (ne 1/4s, e-o 1/4 o).

Morne Plumet the orifice nearest to St. Pierre (that from which the thickest fumes come) is to the east 30° north; the second is 32° north and the third which opens in the ravine is to the east 36° north. St. Pierre lies to the south 10° east [1] at a distance of about 10 kilometers as a bird flies; the town of Prêcheur is about 7 kilometers directly west. The Ruffin house, which is the nearest dwelling, is about 3 kilometers from the upper opening, and 2 kilometers from that situated above La Soufrière; the sugar factory Canonville is 5 kilometers away. From the Grande Rue du Mouillage the upper opening is north 4° east; [2] it is this which is best seen from below and from this escaped the densest vapors; these entirely mask the second opening which in this direction is behind the first; as to the vapors thrown out by the opening situated in the ancient Soufrière, they cannot be seen from St. Pierre; the high crest which separates Rivière Blanche from Rivière Claire hides this opening entirely.

The 29th of August we returned at two o'clock to the Ruffin House. Our excursion had occupied about seven hours; at the cost of some fatigue we bore with us the memory of one of the most imposing spectacles man had ever seen. But our task was not finished. We had to assure ourselves that there were no other points in the mountain where changes had taken place in consequence of the eruption of the fifth of August. Of course it was important to determine what had happened to the hot waters which exist in the part of Mt. Pelée called Montagne d'Irlande where Mr. A. Desnoux de Messirny has built a bath establishment. Sept. 2, Messrs. Le Prieur and Peyraud betook themselves to that locality and found the water of the spring itself at 35°.8, and at the first faucet of the first bath of the establishment (which is ten minutes walk distant) we found the temperature to be 33°. The weather was clear; — after heavy rains have fallen on the pipes, the loss of heat between the spring and the baths is still greater. Dr. Dutroileau who was at the establishment on account of his health on the night of the fifth of August assured us that no change happened to the water

[1] "Du compas" — presumably *magnetic.*
[2] "N 1/4 4 E."

either in temperature, volume or limpidity. The air here as in all the Prêcheur district is strongly impregnated with the odor of sulphuretted hydrogen and all silver pieces turned brown as well as those paintings which contained compounds of lead. In the night of 5th to 6th of August and the 9th of the same month strong but short shocks of earthquake were felt; since that time the earth has remained at rest, but from time to time strong detonations may be heard, similar to cannon shots in the distance. At the same time it is stated that a movement is felt such as might be produced by a powerful blow struck beneath the soil. This sensation was also perceived at the Ruffin House but at my residence Fond Canonville, which is not on the massive rock of the hills but on the seacoast, I perceived nothing of the sort.

All along the road leading to the baths and at the spring Messrs. Le Prieur and Peyraud perceived no landslips, even though the walls of the ravine by this road are formed of tufa 20 to 25 meters in height, frequently deeply trenched. This soil is composed of pumice in masses or fragments on which the water has deposited in certain places incrustations. Above the bathing establishment toward the Carbonal House many rocks are found high up the slope which are friable and fine grained, horizontally bedded, and resting on the fragmentary pumice; these rocks are variously colored and serve as support to the pumice; this suggests that often eruptions had taken place, throwing out pumiceous rocks and that in the intervals the flowing water in its turn had deposited the particles held in suspension during the calm periods. Along the lower part of the road all these beds are very well shown, especially in those portions artificially trenched; there are there several good sized heaps of ancient volcanic cinders of a faint violet tint and rather more sandy in quality than the muds thrown out today; there are no metallic particles; some are reddish like the sands found near the little extinct vents, or on the steep slope back of the vent called La Soufrière.

There remained another important point to determine: namely, what had happened to the actual summit of the Montagne Pelée, where there is a lake supposed to be the seat of an

ancient crater. Seen from St. Pierre the mountain did not appear to have changed at all in height, but had nothing happened to the waters of the lake? No one knew, for no one had been there since the eruption of August 5th, and on this account Messrs. Le Prieur and Peyraud resolved to explore the summit on 4th Sept. The trail to the summit of Mt. Pelée is more travelled than that which leads to the craters. The inhabitants of St. Pierre sometimes make picnic excursions to the summit. Leaving the Eynard House near the base of the mountain, the spur is followed which leads beside and overhangs the ravine of the Rivière Sêche. For three quarters of an hour one passes cultivated lands, the earth there being loose and formed of fragmentary pumice covered by a thin bed of vegetable mold which is very permeable; vegetables are raised on these slopes. Then the traveller comes to the great woods, fig trees covered by vegetable parasites, and long lianas which climb to the very summits of these forest giants and then swing back to earth where they throw out roots and form a dense mass of vegetation entirely distinctive of the tropics. On leaving these woods at the end of an hour, the trees are seen to grow smaller and are gradually replaced by low shrubby and herbaceous vegetation; but none the less the botanist finds here too a constant source of delight. I saw, wrote Mr. Le Prieur, superb flowers worthy of hot-houses, especially two superb cromelias, the one with a long spike of flowers, the other with yellow and red flowers; there are the Brazilian huckleberries, with violet-red flowers; three beautiful species of lobelia, with great flowers which recall some of the fields of certain portions of France. This last plant is found about the lake, and on the humid slopes leading to Morne LaCroix, the culminating point of the mountain — so named because a cross has been placed there. In general, of all the floras of the Antilles, that of Martinique is least known because of the trigonocephalus, whose terrible reputation frightens away the hardiest botanist. Our explorers started at seven o'clock and reached the lake at half past ten. According to the guides who are accustomed to the place no change has taken place in the lake. It is some three hundred paces in circumference; the thermometer gave a temperature in air of 19° and in

the water 20°.5. Nevertheless, the temperature seemed much colder on account of a north wind blowing strongly at the time, and the dense fog over the mountain. This prevented them from viewing the magnificent spectacle ordinarily seen when the weather was fair — a view inclusive from the Grenadines to Antigua. The water of the lake was as abundant and as clear as usual. A maceration within it of certain vegetable matter gives it a grassy taste. Before arriving at the lake it was necessary to cross a crevasse 40 m. wide, which crosses the whole width of the spur that they followed, and is well known to those who have taken this excursion. This crevasse has not been changed at all nor widened. Neither on the road nor from any point of view was any trace of disturbance seen.

The bottom of the lake is carpeted with a layer of thin mud and this rests upon a heap of fragments of pumice of yellowish gray color partly decomposed and recemented by a little ferruginous clay. On the southwest border of the lake a small beach has formed, composed of very fine grains from the debris of these pumiceous rocks which the movement of the waves, raised by the north wind, bring there continually, for there is not on that side any elevation to protect the rocks from the action of the wind. At the summit of Morne LaCroix the barometer gave an elevation of 1277 meters above the level of the sea. This is the highest point of the island. The thermometer in air gave 18°.5 and in earth 19°.2. From this point steam could be seen toward the west, coming out of the upper craters 400 meters lower down. A little more to the left not quite so far down there was seen from time to time a water surface showing bluish reflection, filling the basin called formerly by the guides the "dry pond" (étang sec), because ordinarily this basin is empty.

Even on the plants of the summit of Morne La Croix, traces of volcanic cinders were found which had been carried to this point. Messrs. Le Prieur and Peyraud, not being willing to leave the mountain without a visit to the dry pond — which is commonly believed to be another more ancient crater of the volcano — visited it during their descent by means of a trail rarely used, very difficult and seldom visited before they went

there. They found this supposed "dry" pond filled by a considerable mass of water and according to their estimate five times greater than the upper lake: the guides attributed the presence of this water to the abundant rains which had truly been extraordinary during the "hivernage" of 1851; they asserted that during the previous lenten season this pond had been dry.[1]

The barometer here gave an altitude of 921 meters above the level of the sea. Thus this dry pond is at almost the same elevation as the upper vents of the volcano which are in a ravine beyond. Nothing else was found changed in these localities according to the guides, and nothing in the way of fissures nor disturbances. After this last expedition our official work was finished; we had learned that the action of the volcano did not extend beyond the limits we had explored, and that it was confined to the ravine where the Rivière Claire takes its rise and that immediate vicinity. It was useless to examine the northern slope of mountain toward Macouba, for the inhabitants of that quarter observed nothing extraordinary except an odor of sulphuretted hydrogen, which, it is said, was perceived even as far as St. Marie. At Macouba the leaves of the trees were coated with only the barest trace of those cinders which caused such a fright in St. Pierre.

[1] Some naturalists think that the heat of certain volcanoes comes from no great depth and the water which they throw out is merely rain water which penetrates by means of the fissures in the earth and accumulates in subterranean cavities; several of the observations made during our eruption of the fifth of August lend support to this opinion: (1) the years 1850–1851 had been very rainy, so much so that the dry pond of the mountain has been found full of water and this has become for us a sort of pluviometer; (2) the shocks of earthquake and sensation of bumping under the soil were felt only on the slopes of the mountain, in those little estates situated probably above the level of the seat of volcanic activity — in those which are below this level on the flat land or on the seashore (as at my house in Fond Canonville) although they are still sufficiently near the volcano, nothing of the sort was felt. Moreover at Fond Canonville the springs which escape from the foot of the surrounding hills, like the Fontaine Chaude, have not been in any way changed. It seems to me there is great probability that the volcanic furnace is in the body of the mountain and not at its roots.

Conclusions.

Doubtless no dissertation will be expected from us on the cause and nature of the Mt. Pelée volcano. This study would require a professional knowledge other than we possess; we have merely tried to fulfill the request of the government and report upon the extent of the accidents occasioned by the eruption of the 5th of August and certain exact details. We will vouch for nothing beyond the facts which we ourselves have determined. If these facts, compared with those possessed by science already à propos of the other volcanoes of the earth (more than two hundred in number) can throw some light on the nature of this great phenomenon we shall be well satisfied. But it is not our task to enter upon such matters. The following we can vouch for: —

The eruption of the fifth of August was entirely a local event bounded by the ravine of the Rivière Claire, devastating an area 800 to 900 meters broad at the outside.

The effects of the eruption were at first a continuous buzzing sound, then a series of intermittent detonations, and simultaneously there was thrown out a jet of white or black vapors which made a deposit wherever they spread in the shape of a grayish mud or cinder; and these vapors produce in their vicinity a strong odor of sulphuretted hydrogen.

It is not possible to assert whether this material is always thrown out in the form of cinders or powder, or not sometimes in the form of a rain of mud. It is more probably in a powdery condition and when it falls on the trees it is moistened by steam, or when it falls on the ground it becomes mixed with rain water and forms a sort of clay.

The eruption of the fifth of August was not accompanied by any noticeable earthquake in Martinique, even in the Prêcheur district. Since that time no shocks have been felt. In this respect the opening of these vents seems to be for our island a happy event, a kind of safety valve giving vent to subterranean gases and vapors and so protecting us from those earth commotions which formerly produced such desolation here. "It happens," says Buffon, "that in the lands subject to earthquake,

when a new volcano breaks out earthquakes cease and are only felt during the violent eruptions of the volcano; this has been observed on the island of St. Christopher; and the great encyclopædia begins its article on "volcanoes" as follows: "Volcanoes are a beneficent device of nature, etc. etc."

The buzzing sounds of detonations are not produced by subterranean ebullition, but they take place simultaneously with the ejection of vapor and are produced at the orifice of the vent.

The cinders or muds are the only materials thrown out by the volcano. We have found neither lavas, nor even stones of the smallest possible dimensions which could be identified as eruption products.

The geological structure of Mt. Pelée, as far as our incomplete observations go, shows no lava flows: "for we must not include under the name of lavas," says a geologist, "all the materials ejected from the throat of a volcano such as cinders, pumice stones, gravels, sand; but only those which, reduced by the action of heat to a liquid condition, form on cooling solid masses the hardness of which is greater than marble." These lavas exist principally in the vicinity of volcanoes which eject fire. Now we find about our volcano only pumice, generally fragmentary, and some deposits of cindery substance, in the middle of which appear diorite fragments, torn out of the interior of the earth in preceding eruptions.

This geological structure of Mt. Pelée leads to the belief that the earlier eruptions (which show at least two craters, the dry pond and the lake above) have been of the same nature as that of the fifth of August. Everything goes to show that this volcano should be ranked with the cinder, or mud volcanoes, and not with fire volcanoes (volcans de feu).

Compared with the common notion of the Soufrière of Guadeloupe, what we have learned concerning the new vents of Mt. Pelée is closely similar. It is probable that the conditions are about the same in the case of the Soufrières of St. Lucia, Dominica and Montserrat.

As to Guadeloupe, there have been eruptions several times, notably in February 1837, and December 1846.

These eruptions have always opened new fumaroles and ejected cinders and thick mud.

Mt. Pelée when closely examined shows no fissures, landslips, nor displacement of waters, and hence the action of the eruption of the fifth of August was very local.

The city of St. Pierre situated more than ten kilometers away, and the town of Prêcheur distant seven kilometers, appear to be out of danger from eruptions even considerably greater than the one which has taken place. Nothing in the land where they are situated indicates great catastrophes. Even to reach the Ruffin House or the Eynard House, which are nearest to the vents, a disturbance would be necessary very different from the present one. The matter thrown out even in the immediate vicinity of the vents did not reach a depth of more than a meter. This material finds a natural path of flow in consequence of the steep slope and the gorge of the Rivière Blanche whose waters naturally carry it off to the sea. Further the planters who fled at first have since returned to their dwellings, and their work, and have no further fear of the noises heard from time to time nor of the odor of sulphuretted hydrogen that is continually perceptible.

This odor impregnates the atmosphere all about Mt. Pelée and extends even beyond. It augments or diminishes in certain places according to the direction of the wind; it is sometimes comparable to the odor of burnt gunpowder, at other times to that of stirred up swamp mud; up to this time this odor appears to be merely disagreeable and has had no unsanitary effect either upon men or animals. However, for some time I have been struck with the large number of persons of the Prêcheur district, especially on the habitation Beligny and in my own plantation, who have consulted me about skin troubles and insomnia which they attribute to the sulphurous emanations. I have seen cows drinking the muddy water of the Rivière Blanche and the proprietor assures me that they suffered no ill effects. I have not observed any flight of the birds away from the district though one would suppose their respiratory systems must be very sensitive. Silver pieces in all the estates of the Prêcheur quarter turn brown, and so do all paintings which contain compounds of copper or lead. It is worthy of note that at Guadeloupe the exhalations of sulphuretted hydrogen are not perceived in the

vicinity of the Soufrière — hence we may hope that here also they may cease in due time. No great deposits of pure sulphur have been found either here or in Guadeloupe. Everywhere the sulphur appears to be in a state of combination.

Moreover it should be observed that the presence of sulphuretted hydrogen in the atmosphere in all those localities where there are thermal sulphur waters is not regarded as unhealthy; the waters of Vernet and of Cauterets give out these exhalations and they are believed salutary for people with pulmonary trouble, therefore we may hope that the Prêcheur district, already renowned for its therapeutic qualities in the treatment of these diseases, may acquire a new title to fame in the eyes of such invalids.

But the most remarkable result of our excursions and the most interesting is the information about the place formerly called La Soufrière. There in a very small area four springs of different temperature occur close together, of which three are sulphurous at temperatures of 90°, 70°, and 46°. The other is cold with a temperature of 22.5° and while not being very good to drink is not the less potable. The hot springs contain free sulphuric acid (acide sulphydrique) which volatilizes in consequence of the heat and leaves a residue on evaporation weighing two drachms for each meter of water; this residue of soluble salts contains sulphuric acid and hydochloric acid combined with soda, potash, magnesia, lime and iron as well as a small quantity of silica.

It is to be hoped that at some time when calm shall have been re-established at the seat of eruption, and in the minds of the inhabitants, that some bold speculator will turn to our advantage that which has given us such a fright and will build an establishment of thermal waters in the midst of these places now so desolate. These waters could be conducted to a reservoir so disposed, that their high temperature might be reduced without the loss of their beneficial properties.

Summing up the volcano La Montagne Pelée, it appears to be merely one more interesting curiosity added to the natural history of Martinique — a curiosity that foreigners will wish to visit and which with fitting industry on the part of the natives may

be made a source of health and wealth — in calm weather the ships coming from France will see from a distance the long billow of white vapor rising straight toward the heavens, and will find this a picturesque addition to the landscape — the last touch needed to complete the majesty of our ancient Montagne Pelée.

NOTES AND LITERATURE.

ZOÖLOGY.

Birds in their Relation to Man. — Mrs. Florence Merriam Bailey in her "Birds of Village and Field" included much matter relative to the food of birds, based on the reports of the Dept. of Agriculture; nothing has since been done to put before the public a systematic compilation of the results of the work which this Department has done. Prof. Weed attempted to give a senior class in the New Hampshire Agricultural college a course in economic ornithology. His book "Birds in their Relation to Man"[1] has developed from the series of lectures which he wrote for this object. The work should be an effective agent in informing the general public of the part birds play in the garden, field and forest. Man in his relations to birds comes in for treatment, and it is only thanks to a few honored names such as Wilson, Forbes, Beal and Palmer, that the prevailing record of short-sighted selfishness and ingratitude is lightened.

The book begins with a chapter on methods of studying the food of birds, the only really satisfactory ones being that of the Dept. of Agriculture, the examination of stomachs; and that of Prof. Herrick, the study of nestlings from a tent; the development of the study of economic ornithology is then briefly treated. The next three chapters treat in general the vegetable and animal food of birds; then follow chapters on the amount of food of birds; birds as regulators of outbreaks, and the relations of birds to predaceous and parasitic insects. Nearly half the book is devoted to the food of the separate families of birds as illustrated by typical examples. The bulletins of the Dept. of Agriculture naturally form the basis of this part of the work, with the result that while the passerine orders are well-covered, the food of the water-birds, among which little systematic work has yet been done, is very inadequately treated. Interesting chapters follow on the "conservation" of birds including an account of legislation lately enacted, and helpful suggestions for resisting the attacks

[1] Weed, C. M. and Dearborn, N. *Birds in their Relation to Man.* London. Lippincott. 8vo, pp. 380. With numerous full-page illustrations, cuts, diagrams, etc.

of injurious birds without indiscriminate onslaughts on the whole species. There are four valuable appendices, the first three dealing with protective legislation, the fourth a bibliography of economic ornithology.

There is naturally considerable unevenness of treatment in the account of the food of birds due to the gaps in our present knowledge of the subject, but the matter at Prof. Weed's and Mr. Dearborn's command, is presented clearly and in a scientific spirit. The doubtful birds, the crow, the crow blackbird, the bobolink, etc., are treated in an unprejudiced spirit: — they receive justice tempered with mercy. The book is intended not so much as a storehouse of facts, as a powerful argument, which cannot fail to have a very beneficial influence with the reading public.

The illustrations will give the book a little more favor with the people, and thus are a help. The cuts on pages 137 and on 139, however, are of doubtful value and the full page illustration on page 59 called American Long-eared Owl looks very much like a Short-eared Owl.

R. H.

BOTANY.

The Morphology of Angiosperms.[1]— For several years past there has issued from the Botanical Department of the University of Chicago a series of studies upon the embryo-sac and related topics, some of which have been important contributions to the subject. These papers form the basis of the present volume, which has been prepared by the head of the department, with the assistance of Dr. C. J. Chamberlain. While the book contains little material that has not appeared before, nevertheless it can claim to be based, to a considerable extent, upon work done under the supervision of the authors. Evidently an enormous amount of literature has been gone over, and on the whole, the summarizing of the results has been well done, and the book will be very useful to the student who wishes to know the present status of the subject. One would feel more confidence in some of the conclusions reached by the authors, if these were based to a greater degree upon first-hand observations; but it is quite pos-

[1] Coulter, J. M. and Chamberlain, C. J. *Morphology of Angiosperms.* N. Y. Appleton & Co. 1903. pp. vii + 348.

sible that there is less personal bias than would be the case in a work based mainly upon the personal investigations of the writers.

The title of the book is, perhaps, somewhat misleading, as it deals only briefly with general morphology; but we think the authors have done well to restrict it mainly to the sporangium, gametophyte and embryo, since a general morphology of the vast group of Angiosperms could hardly be compressed within the limits of a single volume.

The book comprises seventeen chapters, of which the first nine will be found of the greatest value to the student for reference. In these the general morphology of the flower, the microsporangium, macrosporangium, male and female gametophyte and embryo are treated in detail, and on the whole extremely well.

The chapter on the flower is in our opinion one of the very best in the book. The author (we assume the senior author) shows here a sureness of treatment which comes only from an intimate first-hand knowledge of his subject, this being by no means so evident in some of the succeeding chapters, especially the one on the microsporangium, which immediately follows this chapter on the flower.

The chapter on the microsporangium opens with the remarkable statement that the *microsporangium* is derived from the periblem. To the reviewer is credited the statement that in Naias the sporangium arises from the plerome — a statement which it may be remarked, he did *not* make. There seems to be a curious confusion in the authors' minds between the terms "sporangium" and "sporogenous tissue."

We cannot accept the view here set forth, that the microsporangium in the Angiosperms is an endogenous structure. The author seems to have in mind the obsolete theory of the imbedding of an originally superficial structure, a view which is directly contrary to the conclusions of the most recent studies on the development of the sporangium. It is now pretty generally admitted that the eusporangiate type, such as that of the angiosperms is the more primitive form of sporangium, and the authors themselves assume the origin of the angiosperms from some form of eusporangiate pteridophyte. The close resemblances in the development of the sporangia between the latter and the angiosperms are familiar to every one who has made a direct study of the subject. We do not believe that the assumed difference in the origin of the archesporium is so fundamental as the authors claim.

It is strange that the most important work of recent years, bearing on the comparative development of the sporangium should be quite ignored. It seems hardly possible that the authors are not

acquainted with Bower's magnificent series of monographs on this subject, but we can find no reference to them in the book.

The idea of an imbedded sporangium seems to have been taken from the older German texts; but a careful study of the context, in either Goebel or Strasburger, will show that both of these authors consider the whole of the superficial tissue of the loculus, as forming the wall of the sporangium, and the whole pollen-sac as the direct homologue of the microsporangium of the pteridophytes.

It seems to be also assumed, although we can see no warrant for this, that the nucellus represents something more than a macrosporangium.

As might be expected, the development of the embryo-sac is given very complete treatment, the chapter dealing with this important topic comprising fifty pages, of which four are devoted to the bibliography. Much of the matter in this chapter is taken from the numerous papers which have been issued from the botanical laboratory of the University of Chicago, and many of the copious illustrations are drawn from the same sources. This chapter will probably be found the most useful in the book. The extensive literature of the subject has been carefully reviewed, and on the whole, little exception can be taken to the references selected to form the bibliography appended to the chapter. A great many facts are presented, and although the very number may be rather confusing to one unfamiliar with the subject, the chapter will nevertheless, give the student an excellent idea of the present status of our knowledge of the development of the embryo-sac.

The male gametophyte, naturally, has less space devoted to it, but is sufficiently complete. We should like to call the authors' attention to a mis-statement. The male prothallium of Sparganium is not referred to at all in the preliminary paper quoted, but was first described in the more complete monograph [1] published subsequently, and which seems to be unknown to the authors.

Chapters seven and nine are concerned respectively with Fertilization, The Endosperm, and The Embryo.

The chapter on Fertilization is well up to date, and gives a clear account of the latest studies upon this important topic. The chapter on the Endosperm is not so satisfactory, a number of more or less important omissions being noted. Thus no mention is made of the peculiar behavior of the lower endosperm nucleus in Naias.

[1] Campbell, D. H. Studies on the Flower and Embryo of Sparganium. *Proc. Cal. Acad. Sci.* Botany, Vol. 1, No. 9, 1899.

The treatment of the embryo is very satisfactory and leaves little to be desired. The discussion of parthenogenesis and polyembryony is especially good.

Except for the chapter on the phylogeny of the angiosperms, the latter chapters might have been entirely omitted without the value of the book being seriously impaired. The chapters on classification are entirely too brief to be of much value to the beginner, and the specialist will prefer to consult Engler & Prantl's *Natürliche Pflanzenfamilien*, from which the substance of these chapters is borrowed.

The chapter on geographical distribution is very fragmentary, and leaves something to be desired, also, in the matter of accuracy. For instance, we doubt whether the statements as to the relative numbers of Archichlamydeæ Sympetalæ and Monocotyledons will bear close examination. Thus the statement that the Archichlamydeæ and monocotyledons are relatively more numerous in the tropics than in temperate regions may be questioned. In round numbers the species of monocotyledons, Archichlamydeæ and Sympetalæ are 20,000, 60,000 and 40,000. A tabulation of the number of species in the Northeastern states is given in Britton & Brown — the numbers are respectively 1058, 1601 and 1361. It is thus seen that while the Sympetalæ are relatively slightly in excess, this is very much more marked in the monocotyledons, which our authors assert are relatively more numerous in the tropics. Two tropical floras were examined, Hawaii and the West Indies. In the former the figures are taken from Wallace's *Island Life*. The numbers are monocotyledons, 137; Archichlamydeæ, 271; Sympetalæ, 318. There is thus a marked predominance of Sympetalæ, and a deficiency of Monocotyledons and Archichlamydeæ, directly the reverse of the statement given by the authors. In the West Indies (Griesebach, *Flora of the British West Indies*) the numbers are approximately, Monocotyledons, 713; Archichlamydeæ, 1456; Sympetalae, 913. The monocotyledons in both cases are relatively less abundant than in the strictly temperate flora of the Northeast United States.

The statement that the Archichlamydeæ have developed no characteristically boreal group, while the Ericales are essentially boreal, is not in accordance with the facts. The authors themselves have called attention to the peculiarly *austral* family of Ericales, the Epacrideæ, and scattered ericaceous genera occur in the tropics, both of the old and new worlds. We should certainly consider the Salicales as quite as distinctively a boreal group as the Ericales.

The chapter on the phylogeny of the angiosperms contains much

of interest, and is clearly written. The recent speculations upon the relation of angiosperms and gymnosperms; the connection between monocotyledons and dicotyledons, are given due attention. In the discussion of the question of the possible monocotyledonous affinities of Podophyllum, it may be said that the suggestion that the two apparent cotyledons are possibly one, *morphologically*, was *not* suggested by Holm. Much stress is laid upon the somewhat dubious "Pro-angiosperms" of the lower Cretaceous. These are supposed to have arisen from some eusporangiate filicineous stock and to have given rise, independently, to the monocotyledons and dicotyledons. If we are to assume that the angiosperms are monophyletic, it is considered that the monocotyledons are probably derivations of the dicotyledons. The recent mutation theory of De Vries is also given due attention.

Prof. Jeffrey's contribution of two final chapters on the vascular system has some value in itself, but comparatively little bearing upon the morphology of angiosperms. Of twenty pages, less than six deal with angiosperms, and of thirty-three figures only five represent this group. These chapters seem to us unnecessarily loaded with technical terms, and are by no means easy reading.

D. H. C.

Notes. — No. 25 of the new series of "Contributions from the Grey Herbarium of Harvard University," issued as No. 5 of the current volume of *Proceedings of the American Academy of Arts and Sciences*, on Sept. 25, is an important paper by Greenman on Mexican and Central American Angiosperms, mostly of recent collection.

An account of an ecological study of Big Spring Prairie, Wyandot County, Ohio, by Bonser, is published as no. 7 of the *Special Papers* of the Ohio State Academy of Science.

Vol. 3, fascicle 1, of Urban's *Symbolæ Antillanæ*, dated September 16, contains the first part of a "Flora Portoricensis," by Urban.

Fascicle 126 of the *Flora Brasiliensis*, issued in December, 1902, concludes Vol. 3, part 5, of the work, dealing with orchids.

The long-delayed number needed to complete the 1901 volume of the *Bulletin de la Société Botanique de France*, dealing with the 1901 session in Corsica, contains important data on the flora of that island, including an especially full account of the fungi.

An account of the vegetation of Corsica, with photograms, by Rikli, is published in the *Viertel-Jahrsschrift der Naturforschenden Gesellschaft in Zürich*, of Apr. 11, 1903.

Vol. 2, fascicle 5, of Coste's *Flore descriptive et illustrée de la France, de la Corse et des Contrées limitrophes*, carries the work into Solanaceæ.

With volume 8, issued in April, 1903, the Rouy, Foucaud and Camus *Flore de France* is brought to a conclusion, and correction sheets for the earlier parts are added to this volume.

An account of the flora of the Sundribuns, by Crain, is published as Vol. 2, no. 4, of the *Records of the Botanical Survey* of India; and from the Government Printing Office at Calcutta is being issued a Flora of the Upper Gangetic Plain, and of the adjacent Siwalik and Sub-Himalayan Tracts, by Duthie. — the first part covering Ranunculaceæ to Cornaceæ.

The first fascicle of an illustrated quarto treatise on the botany of the middle and lower Congo, by de Wildeman, has been issued as a part of the *Annales du Musée du Congo*, of Brussels.

Volume 35 of the *Transactions and Proceedings of the New Zealand Institute*, as is usual with that publication, contains a number of important botanical articles.

Recently issued parts of Engler's *Das Pflanzeureich* are the following: — 12, Pfitzer, Orchidaceæ-Pleonandræ; 13, Ruhland, Eriocaulaceæ; 14, Grosser, Cistaceæ; 15, Mez, Theophrastaceæ.

A paper on root, stem and leaf structure of *Eschscholtzia californica*, by Denniston and Werner, is contained in Vol. 6, no. 8, of *Pharmaceutical archives*.

Under the name *Wittia Amazonica*, Schumann describes and figures in the *Monatsschrift für Kakteenkunde*, of August, a new generic type of cactus from Peru, of the aspect of Phyllocactus but with small red flowers.

The *Revista do Centro de Sciencias, Letras e Artes de Campinas*, of July 31, contains a description and figure of *Rhipsalis pilocarpa*, by Löfgren, and diagnoses and illustrations of a number of other new Brazilian plants by Edwall.

The *Monatsschrift für Kakteenkunde*, of September 15, contains descriptions of several new cacti.

Cereus gummosus, as it grows in Lower California, is figured by Schumann in the *Monatsschrift für Kakteenkunde*, for July 15.

The *Gardeners' Chronicle* of August 8 may be called an Opuntia number, with numerous illustrations of this genus as cultivated at La Mortola.

A cristate tree of *Cereus giganteus*, in situ, is figured by Mrs. Drennan, in *Floral Life* for September.

A good figure of *Yucca glauca*, as it grows in Colorado, is printed in *Floral Life* for August.

Excellent practical instructions for the collection of herbarium material of palms are given by Dammer in the *Notizblatt des K. botanischen Gartens und Museums* of Berlin, of July 10.

A paper on the phylogeny of Angiosperms, resuming publications in the *Botanical Gazette*, is reprinted by Coulter from Vol. 10 of the *Decennial Publications* of the University of Chicago, under date of April 1.

The endogenous adventive buds of several genera of phanerogams are considered by De Candolle in a separate from the *Archives des Sciences Physiques et Naturelles* of Geneva, for July.

The structure of a number of the woods of Borneo is described by Bargagli-Petrucci, and illustrated with photograms, in fascicle 6–8 of *Malpighia* for 1903.

The first part of a study of the comparative anatomy of the barks of the Salicaceæ, by Perrédès, is published as No. 39 of the papers from the Wellcome Chemical Research Laboratories, of London.

The root anatomy of Angiosperms is the subject of a paper by Kroemer, forming Heft 59 of *Bibliotheca Botanica.*

Variation in the androecium of *Stellaria media* is discussed, with curves, by Reinöhl, in the *Botanische Zeitung*, I Abteilung, of September 16.

A paper on the development of the fruits in heterocarpic Composites is published by Patané in *Malpighia*, Vol. 17, fascicle 9.

Dr. Chamberlain's paper on Mitosis in Pellia, contained in the *Botanical Gazette* of July, is concurrently issued from Vol. 10 of the *Decennial Publications* of the University of Chicago.

The application of the kinematograph to the class presentation of plant movements is continued by Miss Scott in a paper on the movements of the flowers of *Sparmannia africana* in the *Annals of Botany* of September.

The spurting of water from the leaf-tips of *Colocasia nymphæfolia* is considered by Molisch in the *Berichte der deutschen Botanischen Gesellschaft* of September 21.

The phenological relations of sun-spots form the subject of a short note, with curves, by MacDowall, in *Nature* of August 27.

An illustrated account of the lumber industry of the Northwest coast, by Lamb, is contained in *Out West* for October.

A nicely illustrated popular article on Elm and Tulip trees, by McFarland, is contained in *The Outlook* of October 3.

An economic account of Zizania, by Brown and Scofield, is published as *Bulletin No. 50* of the Bureau of Plant Industry of the United States Department of Agriculture.

The differentials of varieties of Avena, and those of Triticum, are respectively discussed by Dufour and Dassonville in the *Revue générale de Botanique* of July 12, and Scofield in *Bulletin No. 47* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

An account of rattans and the rattan industry is contained in the *Agricultural Bulletin of the Straits and Federated Malay States*, for April and May last.

An illustrated paper on origin and distribution of camphor in the camphor tree, by Homi Shirasawa, is published in Vol. 5, no. 3, of the *Bulletin of the College of Agriculture* of the Tōkyō Imperial University.

In the *Pharmaceutical Review*, of September, True shows that under the name of Pink-root *Ruellia ciliosa* occurs in the trade, as well as *Spigelia marilandica*.

A well illustrated account of *Castilla elastica* and the Central American production of rubber from it, by Cook, forms *Bulletin no. 49* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

The first of a series of notes on latex-yielding Apocynaceæ of the Congo, by De Wildeman, has been issued at Brussels as a publication of the Independent State of the Congo.

An account of the root-parasitism of the sandal tree, by Rama Rao, is contained in *The Indian Forester* of September.

An account of the Isoetes of southern California is compiled for the *West American Scientist* of September.

Helpful notes on the collection and cultivation of cryptogams for use in the biological laboratory are contained in current numbers of the *Journal of Applied Microscopy and Laboratory Methods*.

An annotated edition of the Codex of Clusius, the original of which appeared three centuries ago, has recently been issued by Istvánffi, of Budapest, and is illustrated by colored reproductions of the original water color sketches of fungi, by Clusius.

A key to the species of Rhizopus, with description of a new parhogenic species, *R. equinus*, is published by Costantin and Lucet in the July number of the *Bulletin trimestriel de la Société mycologique de France.*

A note on Costa Rican edible fungi is contained in No. 24 of the *Boletin el Instituto Fisico geografico de Costa Rica.*

Several edible fungi are illustrated in the *Gardener's Chronicle* of September 19.

Inoculation experiments with graminicolous species of Claviceps are described by Stäger in the *Botanische Zeitung*, Abteilung 1, of July 30.

Some decay of stored apples is shown by Eustace, in *Bulletin No. 235*, and the popular edition of the same, of the New York Agricultural Experimental Station, to be caused in part by a species of Hypochnus following Fusicladium, and in part to be of an obscure origin, without any parasitic cause so far as determined.

Oudemans and Koning have distributed two recent papers on a new Sclerotinia of tobacco, from the Amsterdam Academy.

An economic account of the wilt disease of tobacco, caused by a species of Fusarium, forms the subject of part 1 of *Bulletin No. 51*, of the Bureau of Plant Industry of the United States Department of Agriculture, by McKenney.

An important paper on the bacteria of tilled soil, by Hiltner and Störmer, forms Vol. 3, Heft. 5, of *Arbeiten aus der Biologischen Abtheilung für Land und Forstwirthschaft am K. Gesundheitsamte*, of Berlin.

Bacteria and the Nitrogen Problem is the title of an article by Moore, separately printed from the 1902 *Yearbook* of the Department of Agriculture.

An extended consideration of the significance of bacteriological methods in sanitary water analysis, by Winslow and Nibecker, is contained in the *Technological Quarterly* for September.

An account of the lichens of the northern boundary of Minnesota, by Fink, is separately printed from *Minnesota Botanical Studies*, under date of July 3.

Vol. 4 of De Toni's *Sylloge Algarum*, recently issued, continues the Florideæ.

An account of the algæ which contaminate public water supplies, by Moore, is separately printed from the *Yearbook* of the Department of Agriculture, for 1902.

A most interesting portrait gallery of distinguished botanists is contained in Professor Wittrock's "Catalogus Illustratus Iconothecæ Botanicæ Horti Bergiani Stockholmiensis," issued as Vol. 3, No. 2, of the *Acta Horti Bergiani.*

A portrait of Celakovsky forms the frontispiece to the *Sitzungsberichte der k. böhm. Gesellschaft der Wissenschaften — Mathematisch-naturwissenschaftliche Classe*, for 1902.

A short account of the San Salvador botanical garden is contained in the *Anales del Museo Nacional* of that Republic, of August 1.

A sketch of the botanical gardens at Frankfurt am Main, by Möbius, is separately printed from the 1903 *Bericht der senckenbergischen naturforschenden Gesellschaft.*

The Journals. — *The American Botanist*, for July, contains the following popular articles: — Bradshaw, "The Castor-oil Plant"; Hæselbarth, "The Walking Fern"; and Clute, "Pollination of the Sunflower."

The *Botanical Gazette*, for August, contains the following: — Lawson, "Studies in Spindle Formation"; Frye, "The Embryo-sac of *Casuarina stricta*"; Coker, "The Gametophyte and Embryo of Taxodium — concluded"; Bliss, "The Occurrence of two Venters in the Archegonium of *Polytrichum juniperinum*"; and Cook, "Polyembryony in Ginkgo."

The Botanical Gazette, of September, contains the following articles: — Ganong, "The Vegetation of the Bay of Fundy salt and diked Marshes"; Shull, "Geographic Distribution of *Isoetes saccharata*"; Parish, "A Sketch of the Flora of Southern California"; Thom, "A Gall upon a Mushroom"; and Coker, "Selected Notes, II. — Liverworts."

The Bryologist, for September, contains the following articles: — Gozzaldi, "Thomas Potts James," with portrait; Holzinger, "*Fabroleskea austini* in Europe"; Chamberlain, "Mounting Moss Specimens," and "*Buxbaumia aphylla*"; Harris, "Lichens — Nephroma-Solorina"; Hill, "Branched Paraphyses of *Bryum roseum*"; and Lindberg, "*Stereodon plicatulus*."

The *Bulletin of the Torrey Botanical Club*, for August, contains the following: — Murrill, "The Polyporaceæ of North America — V, The Genera Cyrtoporus, Piptoporus, Sentiger and Porodiscus"; "Mez, Bromeliaceæ Nicaraguenses Novæ"; Berry, "The American Species referred to Thinnfeldia"; Wiegand, "Some Notes on Juncus"; and Nash, "Revision of the Family Fouquieriaceæ."

The *Bulletin of the Torrey Botanical Club*, for September, contains the following: — Best, "Revision of the North American Species of Leskea"; Eastwood, "New Species of Western Plants"; MacDougal, "Some Correlations of Leaves"; and Cushman, "Desmids from Bronx Park, New York."

The Fern Bulletin, for July, contains the following articles: — Fitzpatrick, "The Fern Flora of Iowa"; Clute, "Fernwort Notes, III"; Eaton, "The genus Equisetum in North America, XIV, *E. hiemale*"; Gilbert, "Campbell Easter Waters" (with portrait); Gilbert, "*Asplenium muticum*"; Flett, "The Fern Flora of Washington"; Christ, "Can *Scolopendrium lindeni*, Hook. "be separated from *S. vulgare* Sm.?" and Gilbert, "Two New Varieties of the ternate Botrychium."

The Plant World, for August, contains the following articles: — Safford, "Extracts from the Note-book of a Naturalist on the Island of Guam, IX"; Straw, "Ferns of Smugglers' and Nebraska Notches"; Spaulding, "The Relations of Insects to Fungi"; Barrett, "The Birthplace of Agriculture"; Lindahl, "A fasciated Tulip"; and Waters, "Some Summer Observations."

The Plant World, of September, contains the following articles: — Baum, "The Breadfruit"; Bailey, "Lianes"; Safford, "Extracts from the Note-book of a Naturalist in Guam, X"; Goetting, "The Leucocrinum"; and Barrett, "Three Ecological Problems."

Rhodora, for August, contains the following articles: — Fernald, "American Representatives of *Luzula vernalis*"; Phelps, "An Hour in a Connecticut Swamp"; Webster, "A Beautiful Pluteolus";

Collins, "Some Notes on Mosses"; Eames, "The Dwarf Mistletoe in Ct."; and Collins, "Notes on Algæ, V."

Rhodora, for September, contains the following articles: — Eames, "The Dentarias of Connecticut"; Collins, "Isaac Holden"; Cushman, "Notes on New England Desmids, I"; Fernald, "*Arabis drummondii* and its relatives"; Collins, "Notes on Algæ, VI"; Robinson, "On the Twelfth List of New England Plants"; and a short notice of the late Charles James Sprague.

Torreya, for September, contains the following articles: — Berry, "Liriodendron Notes"; Robinson, "The Distribution of *Fucus serratus* in America"; Earle, "Key to the North American Species of Galera"; Richards, "An improvised horizontal Microscope"; Griggs, "A remarkable Physalis"; Cockerell, "Two Orchids from New Mexico"; Small, "The Habitats of *Polypodium polypodioides*"; and Barnhart, "Duplicate Binomials."

CORRESPONDENCE.

To the Editor of the American Naturalist:

Sir:— In *The American Naturalist* June, 1903, p. 385, Mr. J. H. Powers says that the metamorphosis of *Amblystoma tigrinum* is due to nutritive causes. Be pleased to rectify that the same conclusion was published by me August, 1899, in *La Naturaleza*, Ser. ii, F. iii, p. 369. The title of my notes is as follows:

"El Ajolote sufre la metamorfosis general en la clase de los batracios, par aumento de nutricion y no por cambia de medio."

Experiments and observations in the latter where Amblystoma was first observed, show that metamorphosis is very slow in artificial or natural conditions, if the animals are feeble, and very rapid in the best conditions of nutrition as in deep waters of Xochimilco, a lake that never becomes dry.

The dogmatical views on adaptation of Amblystoma are wrong and the paper of Mr. Powers has only attested my own published conclusions.

I am very respectfully yours,

A. L. Herrera.

Mexico, Oct. 12, 1903.

PUBLICATIONS RECEIVED.

(Regular exchanges are not included.)

BACON, E. M. Boston, A Guide Book. Prepared for the Convention of the National Educational Association, July 6–10, 1903, etc., etc. Boston, Ginn & Co., 1903. x + 190 pp., maps and illustrations.— BAKER, F. C. Shells of Land and Water. A Familiar Introduction to the Study of the Mollusks. Chicago. A. W. Mumford, 1903. 8vo, xvii + 175 pp., 8 colored pls. and many text figs.— BURKETT, C. W. STEVENS, F. L. and HILL, D. H. Agriculture for Beginners. Boston, Ginn & Co., 1903. 8vo, xii + 262 pp., 215 figs. — COMSTOCK, ANNA B. Ways of the Six-Footed. Boston, Ginn & Co., 1903. 8vo, xii + 152 pp., 47 figs.— DODGE, C. W. General Zoölogy. Practical, Systematic and Comparative. Being a Revision and Rearrangement of Orton's Comparative Zoölogy, New York, American Book Co., 1903. 8vo, 512 pp., 379 figs. $1.80.—GARDINER, J. S. The Fauna and Geography of the Maldive and Laccadive Islands. Being the Account of the Work Carried on and of the Collections made of an Expedition during the years 1899 and 1900. Vol. ii, Part 1, pp. 473–588, pls. 26–34.— HIGGINSON, E. Map of the Republic of Peru. London. 1903.— HUNTER, S. W. and VALENTINE, M. C. Laboratory Manual of Biology. New York, Henry Holt & Co., 1903. 8vo, xii + 215 pp.— JONES, L. H. The Jones Readers 1–5. Boston, Ginn & Co., 1903. 8vo, 1, 160 pp.; 2, 208 pp.; 3, 286 pp.; 3, 416 pp.; 5, 496 pp. Many illustrations, partly colored.— KELLOGG, V. L. First Lessons in Zoology. .New York, Henry Holt & Co., 1903. 8vo, x + 363 pp., 257 figs.— MILLER, D. R. The Criminal Classes. Causes and Cures. Dayton, United Brethren Publishing House, 1903. 8vo, ix + 227 pp., portraits. $1.50 — MORELEY, MARGARET W. The Insect Folk. Boston, Ginn & Co., 1903. 8vo, vi–204 pp., many figs. NOÉ, J. Recherches sur la vie osscillante. Essai de biodynamique. Paris, Alcan, 1903. 8vo, 372 pp., 40 figs. 7 francs.— WATERS, C. E. Ferns. A manual for the Northeastern States with analytical keys based on the Stalks and on the Fructification. New York, Henry Holt & Co., 1903. 8vo, xi + 362 pp., over 200 figs. $3.00.— WELCKER, A. A Dream of Realms Beyond Us. San Francisco, Cubery & Co., 1903. 8vo, 38 pp.— WUNDT, W. Naturwissenschaft und Psychologie. Leipzig, Engelmann, 1903. 8vo, 126 pp., 3 marks.

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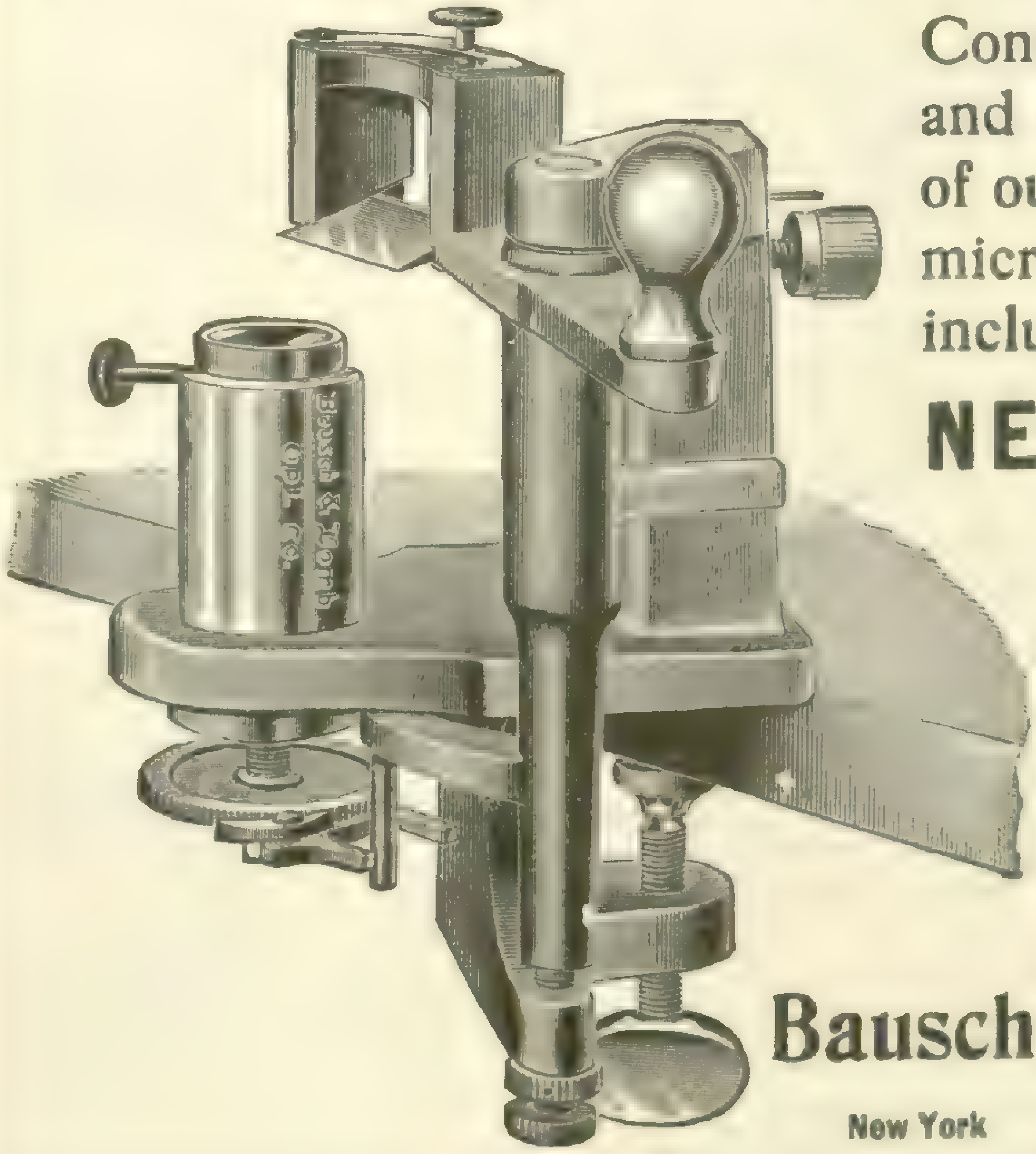

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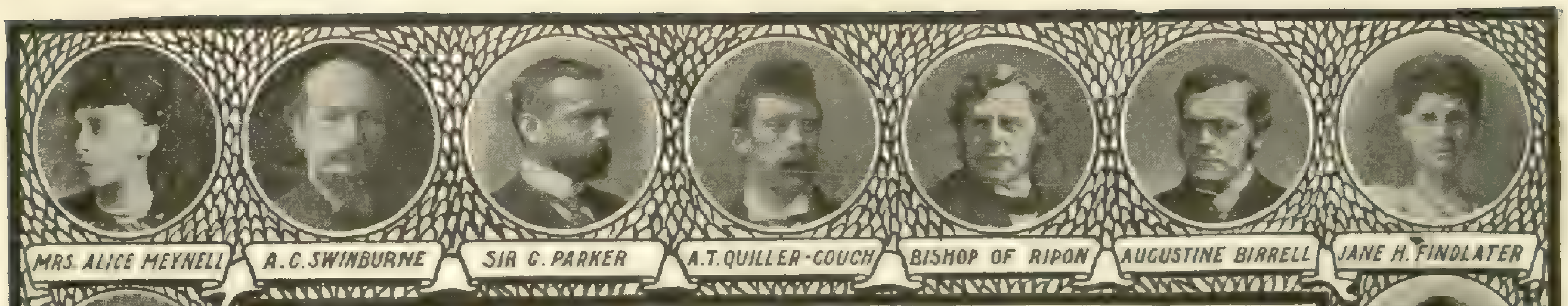

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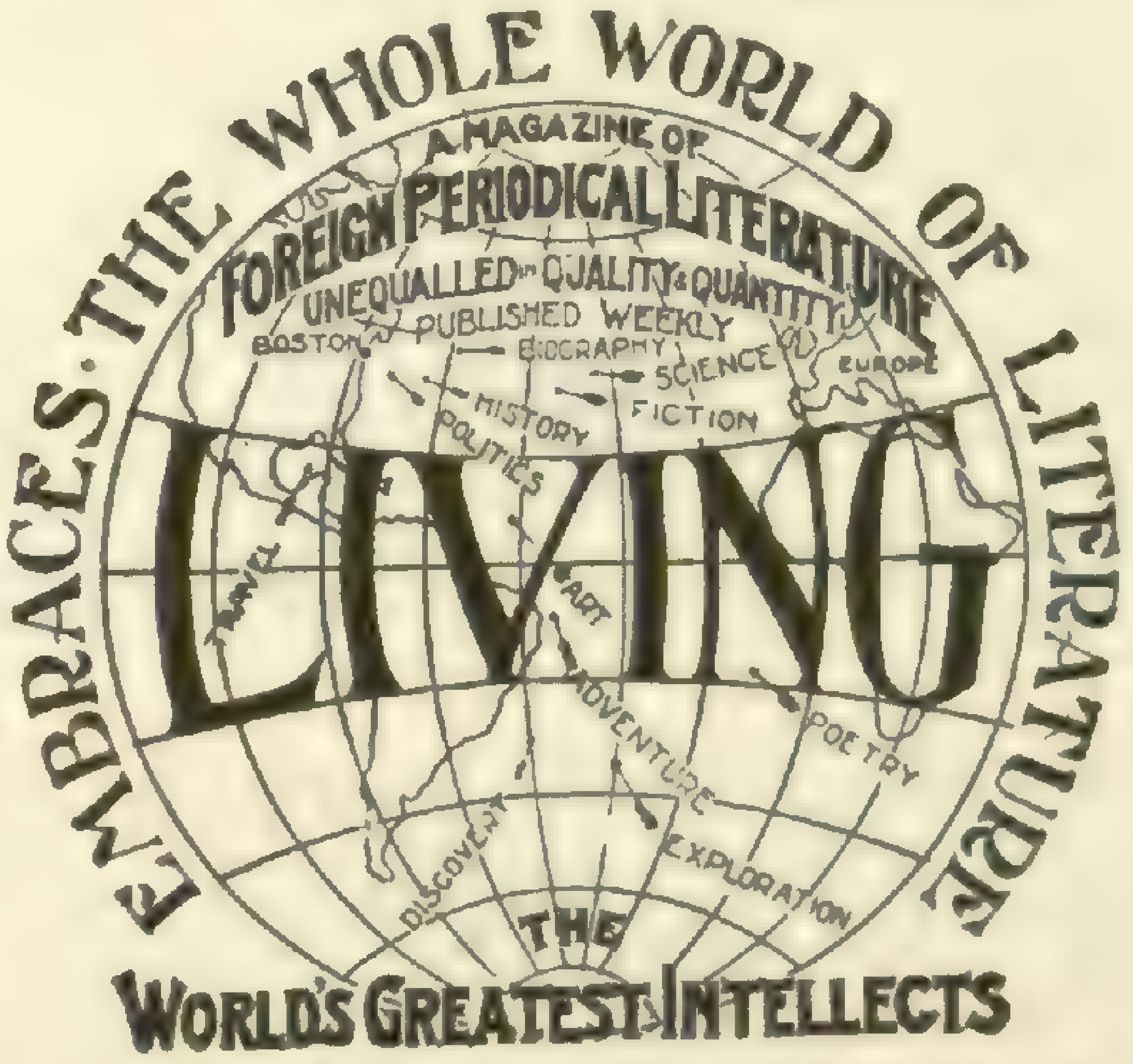

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RECLASSIFICATION OF THE REPTILIA.

HENRY FAIRFIELD OSBORN.

HISTORY OF CLASSIFICATION.[1]

Philosophy of Classification.— The history of the classification of the Reptilia resembles that of the classification of other forms of vertebrates in its gradual approximation to the truth.

The general progress has been from superficial to profound characters, from purely adaptive characters to those which are phylogenetic and indicate real affinity. For a century and a half superficial resemblances and analogous adaptations have been the pitfalls out of which the final classification is slowly emerging.

Every classification, moreover, has had its underlying philosophy. The "special creation" philosophy underlays the Linnæan system, but in so far as Linnæus, Cuvier, De Blainville, Owen perceived a real order in certain profound characters, their systems will stand.

The philosophy underlying modern classification is the

[1] Presented at the first meeting of the Society of Vertebrate Palæontologists, Philadelphia, December 29th, 1903. Abstract, in part, of a memoir entitled The Reptilian Subclasses Synapsida and Diapsida and the Early History of the Diaptosauria. *Mem. Amer. Mus. Nat. Hist.* Vol. I, Pt. VIII, Nov. 1903.

Lamarck-Darwin theory of the law of descent which involves a branching or phylogenetic scheme of relationships. Toward this we are slowly progressing. The final classification will be a formal or tabular statement of the tree of descent, in which only so much pre-Darwinian classification will survive as was based upon the perception of real phylogenetic characters.

The evolution philosophy held out a strong temptation to rapid generalization in phylogeny. It is a striking fact that the evolutionists, Huxley, Cope, Hæckel, perhaps because they attempted to generalize too rapidly, have proved less fortunate in their arrangement of the Reptilia than Owen, whose pre-Darwinian systems of 1839 and 1859 have best stood the test of time and of discovery.

Both Cope's and Huxley's systems are largely wrecks today; Huxley's because while entirely logical in method it outran the state of knowledge and discovery. Cope was less logical; his fatal error was over reliance on single characters without discriminating whether they were primitive or adaptive. Marsh was gifted with unerring taxonomic judgment as to real phylogenetic relationships; the chief defect of his system was that he partly or wholly ignored the rules of priority, renaming and redefining groups which had previously been defined with sufficient clearness to be recognized. It is with real regret that I feel compelled, as a matter of historic justice, to revive some of the older names for certain groups of which our knowledge is almost entirely due to the fundamental contributions of Marsh.

Priority.— Palæontological discovery is constantly swelling and expanding the groups of fossils discovered long ago; it is consequently necessary either to abandon these groups or to raise or lower their grade. For example, Owen's "family" Cynodontia has become a suborder, his "families" Dicynodontia and Theriodontia have become orders, his "orders" Anomodontia and Dinosauria have become superorders.

If we should confine each group to the rank or systematic position originally assigned to it by its author in a very limited state of knowledge, we should have to rename the larger number of groups, and this certainly is not advisable either in the interest of clearness or as a matter of historic justice.

The history of classification is usually presented by giving the complete schemes published successively by various anato-

FIG. 1.— A primitive Plesiosauroid Synapsidan, *Lariosaurus balsami*. After Boulenger. × ½.

mists. The student will perhaps gain as valuable a lesson by considering the anatomical philosophy, true or false, which has prompted different systems of classification.

False Principles of Classification.

Superficial Resemblances.— In Brogniart's system of 1799 the Lacertilia and Crocodilia are wrongly united on limb structure as (II) Saurii, as distinguished from (III) Ophidii, and (I) Chelonii.

The similar scaly covering led Latreille (1820) to rightly unite the Ophidia and Lacertilia as Squamosa ; previously Oppel (1811) grouped the Lacertilia and Ophidia as Squamata ; this, however, is the single instance in which epidermal resemblance happens to coincide with underlying fundamental characters.

As instances of errors based upon epidermal characters, we may cite the union of the Testudinata and Crocodilia by Klein as Cataphracta ; or the union of the same animals by Merrem as Loricata.

Resemblances in Single External Organs.— So able a palæontologist as von Meyer (1830) attempted to classify the reptiles by resemblances in foot structure. He thus divided the Saurii, or limbed reptiles into (1) Dactylepodes, including Lacertilia and Crocodilia ; (2) Nexipodes, including the Ichthyosauria and Sauropterygia (*Plesiosaurus, Nothosaurus*) ; (3) Pachypodes, including the Iguanodontia and Megalosauria ; (4) Pterodactylii, including the Pterosaurs — a false system.

Classification of Analogous Adaptations.— De Blainville (1835) united the Ichthyosauria and Sauropterygia as Enaliosaurii, or sea lizards. Owen (1839) adopted the order Enaliosauria as embracing the Ichthyopterygia (1859) and Sauropterygia (1859), but remarked that these animals "do not form a strictly natural group."

Classification by single Internal Characters.— This method was especially characteristic of Cope. In 1869 he defined the Archosauria as differing from the Monimostylica of Müller only by the exclusion of the order Testudinata ; he observed that close sutural attachment of the quadrate bone "was the important feature which characterizes the order" ; by this feature he united the Sauropterygia (Nothosaurus, which was selected as a type) the Crocodilia, the Thecodontia (suborder of Dinosauria), the Dinosauria, the Anomodontia, and the Rhynchocephalia ; a totally unnatural and transitory grouping, because based upon

the possession of a single primitive character, namely, the *fixed quadrate*.

We find that almost every attempt to classify the reptiles by superficial characters, by external organs, by general external adaptations, by single internal organs, has proved unnatural.

True Principles of Classification.

The conclusion is that there are three ruling principles in classification.

First, as to *priority*, we owe it to our palæontological forebears not to abandon the lower or higher groups they have proposed except in cases of absolute necessity. In some instances we must give a group a higher or lower rank than the author originally assigned to it, or a different position in the system. Priority has no force where a group is based on a false conception or on a false grouping of types, as in the definitions of Theromorpha and Archosauria by Cope.

Second, as to *phylogeny*, classification is a formal expression of our knowledge of phylogenetic relationships; it must, therefore, constantly shift and change as new relationships are discovered. The final classification will be the phylogenetic tree. This being the case, it is desired to include within a group its ancestral forms as soon as they have definitely branched off toward it. For example, Hyracotherium should not be placed in the Lophiodontidæ, as was done by Cope, but in the Equidæ. Again, if it should be demonstrated that the Protorosauria are ancestral to the dinosaurs and to no other reptiles, they should be placed in the superorder Dinosauria.

Third, as to *definition*, classification, like phylogeny, should be based on a number of characters of different parts of the body having different functions, in order to diminish the danger of being misled by analogous evolution, otherwise known as parallelism, convergence and homoplasy.

The neglect of one or other, and in some cases of all these three principles and the loss of the clarifying mind of George Baur have led to great and rapidly increasing confusion in the arrangement of the Reptilia in recent years. Smith Woodward, Broom and von Nopsca, have been working in the right direction.

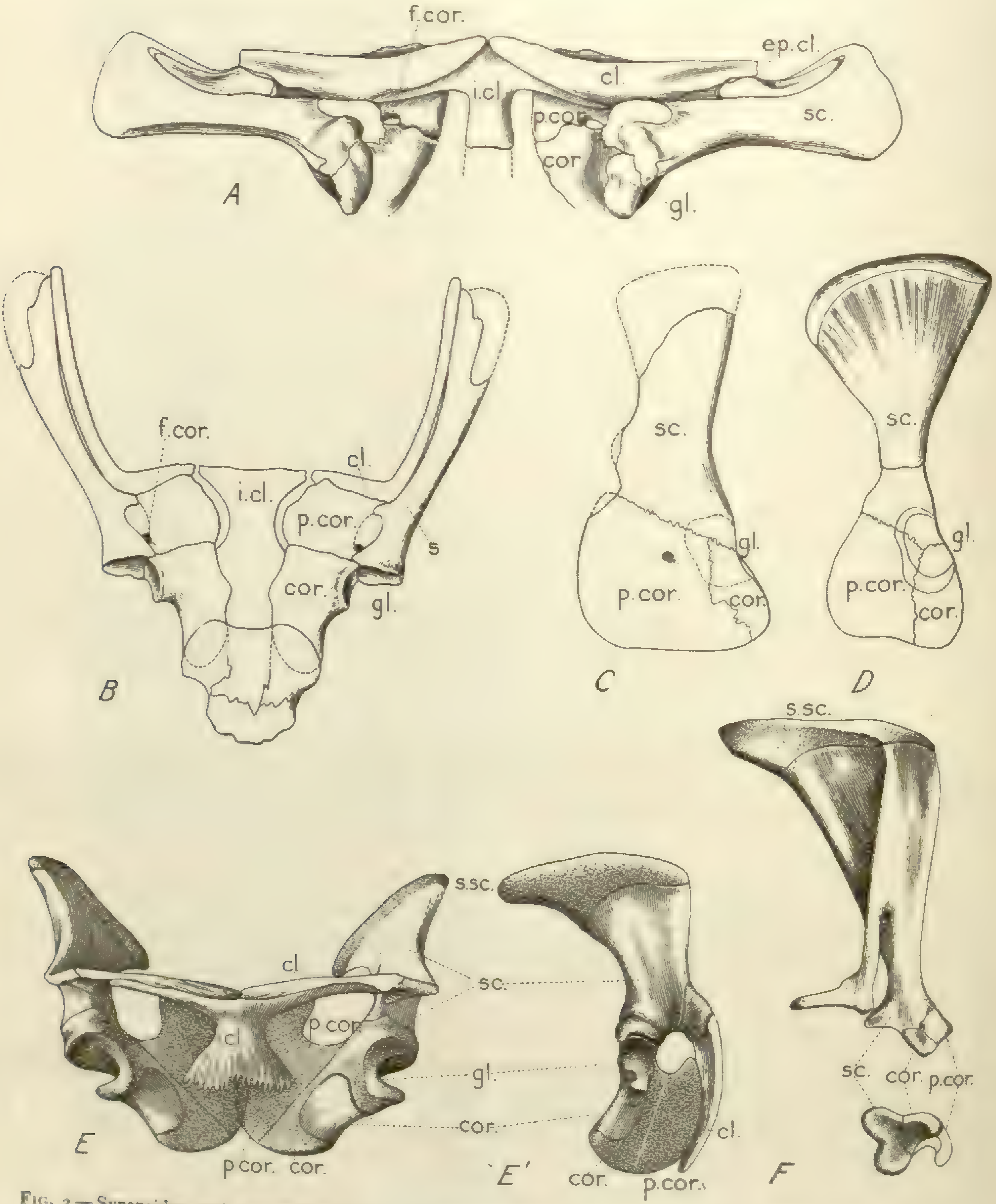


Fig. 2 — Synapsidan and mammalian types of shoulder-girdle. *A–D*, after Seeley; *E–F*, after Howes. *A*, *Pareiasaurus bainii*; *B*, *Keirognathus cordylus*; *C*, Deuterosaurus; *D*, Rhopalodon; E, ventral, *E'*, lateral views of Ornithorhynchus; F, Lepus.

Proposed Reclassification.

At the Washington meeting, 1902, of the American Association, I presented a joint paper with Dr. J. H. McGregor on the diphyletic arrangement of the reptiles, based on comparison of a large number of characters. I have since made a more searching study of the same problem, designating these two groups as the subclasses Synapsida, or primitively single-arched reptiles, and Diapsida, or primitively two-arched reptiles, and have grouped all the most primitive forms of Diapsida in the superorder Diaptosauria, a group equivalent in taxonomic rank to the Squamata or the Dinosauria. I now propose to briefly describe the reptiles which fall within these two groups.

SUBCLASS SYNAPSIDA Osborn.

The chief distinction of the single arched reptiles is that there is either no opening at all in the temporal region (Cotylosauria), or a single large supratemporal opening (Anomodontia, Plesiosauria, Testudinata) as in the upper view of the skull of a plesiosaur, a turtle, or a mammal. This supratemporal fossa is large, because the cranium or brain case is long while the facial portion of the skull is relatively short, these proportions being directly reversed in the Diapsida. The temporal arch consists primitively of two arches combined. The squamosal is always a large element. The quadrate is correspondingly more or less reduced; it is never movable, and is functionally supported by the squamosal. In the shoulder girdle the coracoid and procoracoid are separate, or united by suture. The phalangeal formula is primitively 2. 3. 3. 3. 3, like that of mammals.

I. *Order* Cotylosauria Cope

Pareiasauria Seeley.

These are the most primitive of reptiles, retaining many Stegocephalian (amphibian) characters, and a solid cranial roof with temporal openings rudimentary or not developed at all.

Subclass **SYNAPSIDA** Osborn 1903.
Order COTYLOSAURIA Cope 1880 (Pareiasauria Seeley 1889)
Superorder ANOMODONTIA Owen 1860. (Theromorpha Cope 1878, in part.)
- Order THERIODONTIA Owen 1876.
  - Suborder Therocephalia Broom 1903.
  - Suborder Cynodontia Owen 1861.
- Order DICYNODONTIA Owen 1860.

Order PLACODONTIA *auct. ex* H. von Meyer[3] 1863 Incertæ Sedis.
Order SAUROPTERYGIA Owen 1860.
- Suborder Simosauria *auct. ex* Gervais[1] 1845. (Nothosauria Seeley 1882.)
- Suborder Plesiosauria *auct. ex* Quenstedt[2] 1852.

Order TESTUDINATA *auct. ex* Shaw[4] 1802.
- Suborder Pleurodira *auct. ex* Duméril and Bibron[5] 1835.
- Suborder Cryptodira *auct. ex* Duméril and Bibron[6] 1835.
- Suborder Trionychia[7] *auct. ex* Pictet 1853.

Subclass **DIAPSIDA** Osborn 1903.
Superorder DIAPTOSAURIA Osborn 1903.
- Order PROCOLOPHONIA Seeley 1867.
- Order PROTOROSAURIA Seeley 1887.
- Order PROGANOSAURIA Baur 1887.
- Order GNATHODONTIA Owen 1680. (Rhynchosauria Osborn 1903).
- Order PELYCOSAURIA Cope 1878.
- " CHORISTODERA Cope 1877.
- " RHYNCHOCEPHALIA Günther 1868.

Order PARASUCHIA Huxley 1875.
- Suborder Aëtosauria Nicholson and Lydekker 1889.
- Suborder Phytosauria Baur 1894 *ex* Jaeger 1828.

Order ICHTHYOSAURIA Blainville 1835 *ex* Jaeger 1824. (Ichthyopterygia Owen 1860.)
Order CROCODILIA[9] Wagler (?) 1830.
- Suborder Mesosuchia Huxley 1875.
- Suborder Eusuchia Huxley 1875.
- " Thalattosuchia Fraas 1901.

Superorder DINOSAURIA Owen 1840.
- Order THEROPODA Marsh 1881.
  - Suborder Megalosauria *ex* Fitzinger 1843. (Thecodontia Owen 1860.)
  - Suborder Symphypoda Cope 1867. (Compsognatha Huxley 1870.)
- Order OPISTHOCŒLIA Owen 1860. (Sauropoda Marsh 1881.)
- Order ORTHOPODA Cope 1866. (Predentata Marsh 1894.)

Superorder SQUAMATA Oppel 1811.
- Order LACERTILIA[9] Owen 1839.
- Order MOSASAURIA *auct. ex* Gervais[8] 1845.
- Order OPHIDIA[9] Brogniart 1802.

Order PTEROSAURIA *auct. ex* Kaup 1834.

[1] "Simosauriens."
[2] "Plesiosauri."
[3] "Placodonten."
[4] "Testudines."
[5] "Pleurodères."
[6] "Cryptodères."
[7] "Trionychides."
[8] "Mosasauridés."
[9] The dates and authors assigned for the earliest recognition of the supergeneric rank of several of these groups may be altered by future investigations.

The large South African Pareiasauridæ are more specialized than the Texan Pariotichidæ and Diadectidæ, the latter being the type of the order.

Theoretically some unspecialized members of this order gave rise to all other reptiles including both Synapsida and Diapsida.

II. *Superorder* ANOMODONTIA Owen.

This was originally defined by Owen (1860) as an 'order' embracing the "families" Dicynodontia, Cryptodontia and Gnathodontia (Rhynchosaurus). The reference of the latter 'family' proves to have been an error. In 1861, in the second edition of his *Palæontology*, Owen included in the Anomodontia the 'family' Cynodontia, based on the types Galesaurus and Cynochampsa; thus raising the Anomodontia to the rank of a superorder which is equivalent in part to the superorder Theromorpha Cope.

This 'superorder' includes two orders, which represent an adaptive radiation from more primitive truly reptilian types (Therocephalia Broom) into the more mammal-like Cynodontia, both with full sets of teeth, and finally into the highly specialized Dicynodontia, in which the teeth are greatly reduced. All these animals retain, however, some primitive or cotylosaurian and stegocephalian characters.

I. *Order* THERIODONTIA Owen.

1. *Suborder* Therocephalia Broom.

Broom has recently published an admirable paper on the "Classification of the Theriodonts and their Allies,"[1] in which the Therocephalia[2] are defined from the types Scylacosaurus, Ælurosaurus, Ictidosuchus, Deuterosaurus, Titanosuchus, Gorgonops, as representatives of six families. These are medium sized reptiles, and apparently the most primitive of the Anomo-

[1] *Rep. So. Afr. Assoc. Adv. Sci.* 1903, pp. 362–369.

[2] This is defined as an order by Broom and may prove to be of full ordinal rank; it is here provisionally grouped with the Anomodontia as a suborder of Theriodontia.

dontia. The teeth are differentiated as in mammals into incisors, canines (sometimes double), and molars; the molars, however, are simple, and the palate is simple, like that of the Cotylosauria, that is, there is no secondary palate.

2. *Suborder* Cynodontia Owen.

This was originally defined as the "family" Cynodontia by Owen in 1861, and may be embraced within the order "Therio-

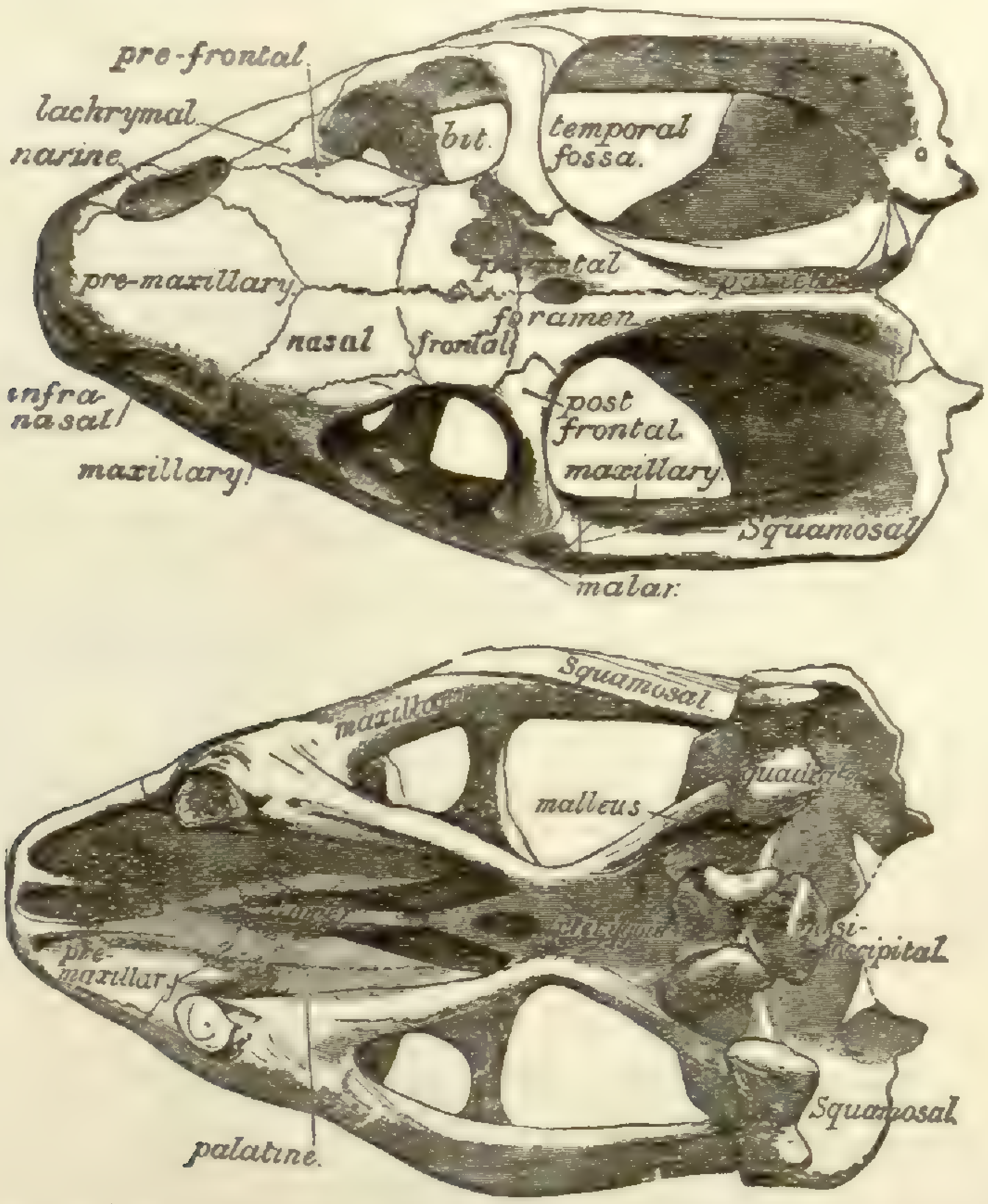


FIG. 3.—Synapsid Type. Palatal and superior views of the skull of Dicynodon, showing the elements as interpreted by Seeley. Note especially the exposure of the prevomer, the large extension of the squamosal, the pre- and postfrontals, the single squamoso-maxillary bar. After Seeley.

dontia" Owen of 1876, which was based on the same types, viz.: Galesaurus and Cynochampsa.

These are intermediate anomodonts of medium size. In contrast with the Therocephalia the squamosal is more expanded and the quadrate is greatly reduced. Approaching the mammals also, there is the secondary palate, formed of the maxillaries and palatines, also the double condition of the occipital condyles

which are single in Therocephalia. These cynodonts have lost several of the other more primitive characters of the therocephalians, such as teeth in the palate; and their specialization is in the direction of the mammalia. The phalangeal formula is 2. 3. 3. 3. 3. They include three families, typified respectively by the genera Lycosaurus, Cynognathus, and Gomphognathus.

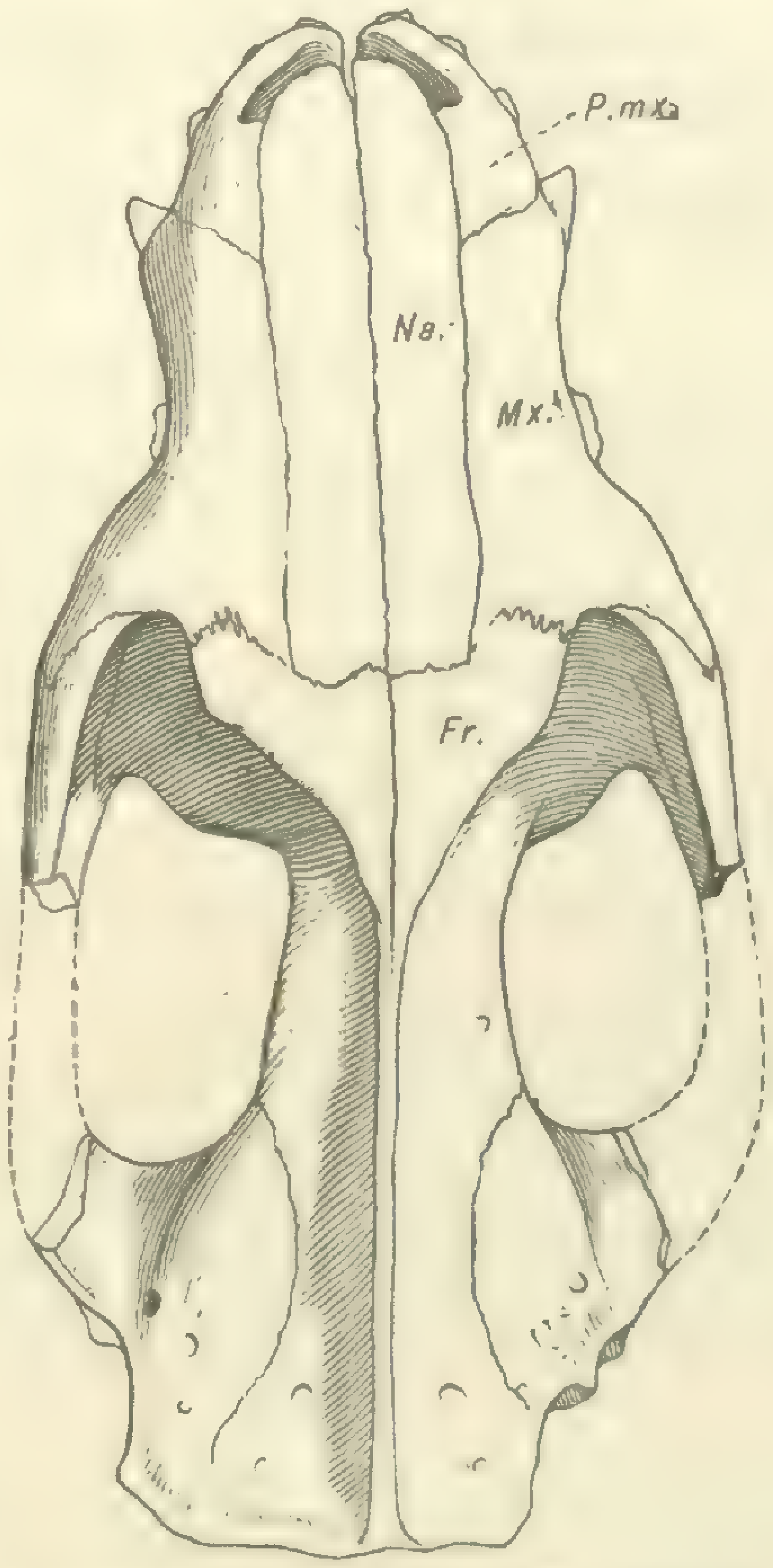


FIG. 4.— Synapsid Type Top view of the skull of a primitive amblypod ungulate, Pantolambda. × ½.

2. *Order* DICYNODONTIA Owen.

This term was originally used as a "family" term, under Anomodontia, by Owen in 1859; Huxley raised it to the rank of an order from the types Dicynodon, Oudenodon. The latter, Owen (1859) had placed in the "family" Cryptodontia, in reference to the absence of teeth. Despite the high specialization of the dentition, these animals retain the more primitive features of the single condyle, of the cleithrum or epiclavicle, of the large quadrates. On the other hand, like the cynodonts, they show a rudimentary secondary palate. They approach the mammals also in the loss of the prevomers and development of the vomer (parasphenoid).

In the most primitive family of Endothiodontidæ one or more series of molar teeth are present on the maxillaries and dentaries; the interclavicle is a rounded plate as in the Stegocephalia. In the more specialized Dicynodontidæ, maxillary teeth are absent, or present as a pair of tusks, and there are no teeth in the lower jaw; the interclavicle is elongated, and a cleithrum is present. The third family, Lystrosauridæ, exhibits a small interclavicle, and no cleithrum. A fourth family, Cistecephalidæ is doubtfully ranked here by Broom.

Broom has contributed a large number of papers on the structure and arrangement of the South African reptiles, which for the first time throw a perfectly clear light on their relationships to each other.

FIG. 5.— Synapsid Type. Dorsal aspect of skull of *Nothosaurus andriani?* A primitive plesiosauroid reptile. After Cope.

3. *Order* PLACODONTIA.

(*Incertæ sedis.*)

The position of this order as typified by the genus Placodus, is still very doubtful. It is characterized by very large teeth in the palate, and by the absence of teeth on the maxillaries and premaxillaries. It includes littoral, shell-eating forms, which may be an independent offshoot of the Anomodontia, or may be more nearly related to the Sauropterygia.

III. *Order* SAUROPTERYGIA Owen.

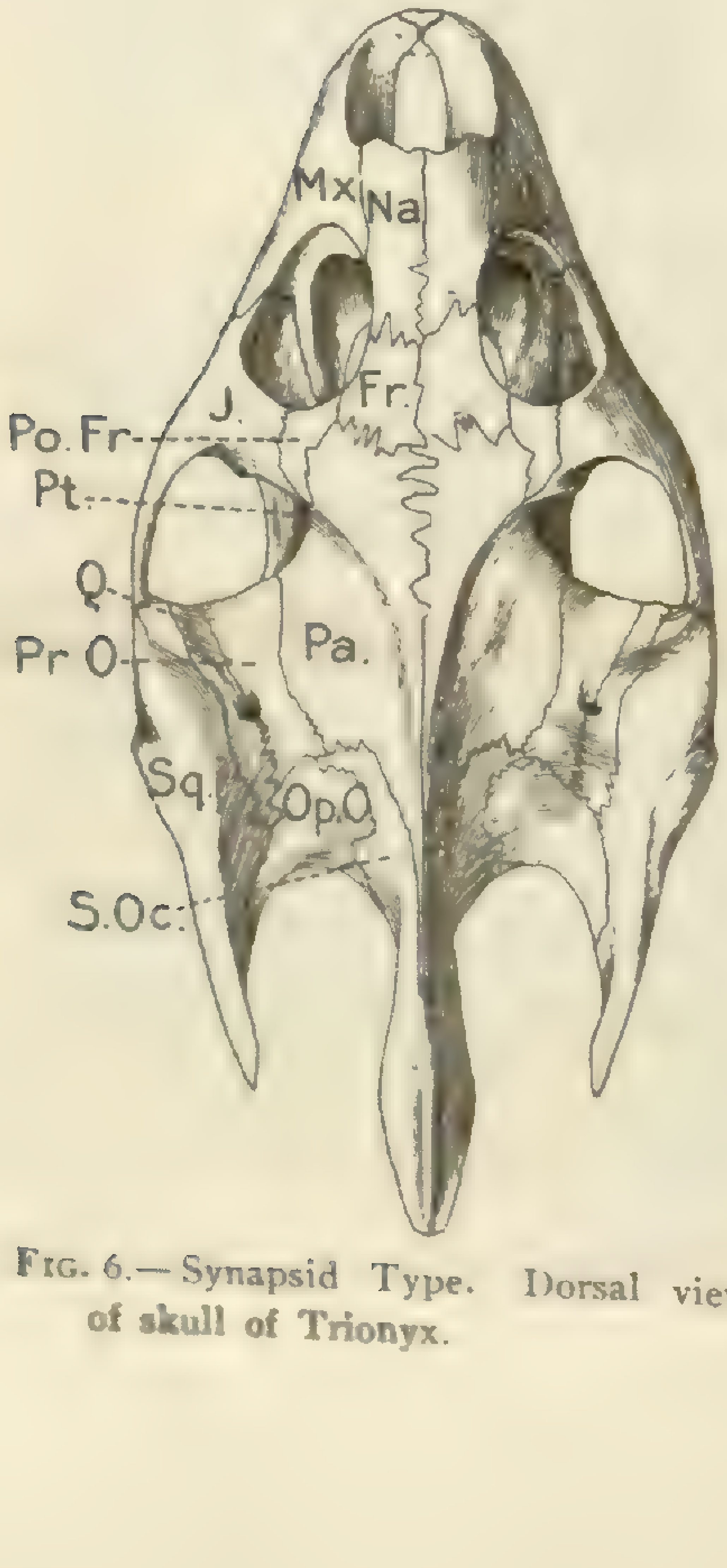


FIG. 6.— Synapsid Type. Dorsal view of skull of Trionyx.

The theory of the relationship of the plesiosaurs to the Synapsida and especially to the Anomodontia and Testudinata still requires confirmation. The skull structure is typically synapsidan. The shoulder girdle structure, so far as known, in the Triassic plesiosaurs is certainly more synapsidan than diapsidan. Numerous resemblances to the Testudinata have been pointed out. On the other hand, certain of the oldest Triassic plesiosaurs, such as Lariosaurus, (Fig. 1) closely approach the Diapsida in the phalangeal formula.

IV. *Order* Testudinata (*ex* Shaw.)

The kinship of the Testudinata to the Synapsida is indicated both by the skull structure and by the phalangeal formula. The shoulder girdle structure, like that of the plesiosaurs, is still in dispute; the main question being as to the homologies of the

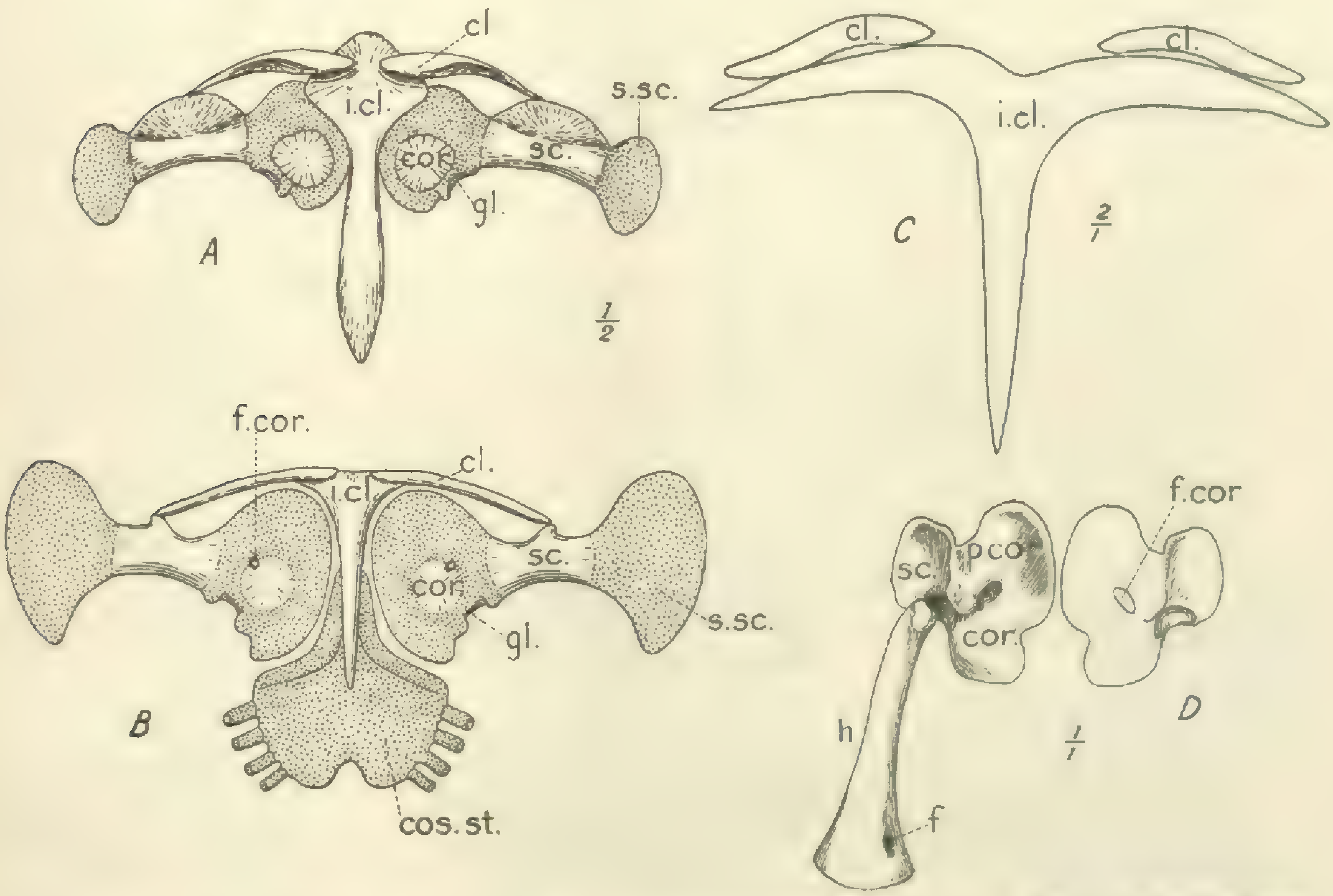


Fig. 7.—Diapsidan types of shoulder-girdle. *A*, Palæohatteria. After Credner. The cartilaginous areas are entirely restored. Restoration by J. H. McGregor. × $\frac{1}{2}$. *B*, Sphenodon juv. (15 cm.); modified from Howes. By J. H. McGregor. × $\frac{8}{1}$. *C*, Pleurosaurus. Cartilaginous elements omitted. After Dames. × $\frac{2}{1}$. *D*, *Mesosaurus tenuidens*. Modified from Gervais. × $\frac{1}{1}$.

Cl, clavicle; *i. cl*, interclavicle; *sc*, scapula; *s. sc*, suprascapula; *cor*, coracoid; *p. cor*, procoracoid; *f. cor*, coracoid foramen; *h*, humerus; *f*, entepicondylar (ulnocondylar) foramen.

anterior ventral processes variously known as the "procoracoid" or "proscapula."

SUBCLASS DIAPSIDA Osborn.

All these animals are readily distinguished by their general likeness to the existing Hatteria. In contrast to the Synapsida the cranium is short; the temporal region is primitively fenestrated by two distinct openings, the supra- and latero-temporal fenestræ,

bounded by the supra and latero-temporal arches, one or both of which may secondarily disappear. In further contrast with the Synapsida, the squamosal is a relatively small element, frequently separate from the prosquamosal, and never entering into articulation with the lower jaw; the quadrate, on the other hand, is a relatively large element, uncovered, and sometimes secondarily movable. In the shoulder girdle we find a most distinctive character in the early coalescence of the coracoid and procoracoid into a single bone, or in the degeneration of the procoracoid. Another highly distinctive character is the phalangeal formula, 2. 3. 4. 5. 3–4, which is secondarily modified in the aquatic forms.

There appear to have been two great adaptive radiations among the Diapsida. The *first* is that which occurred during the upper Carboniferous and Permian, branches of which are

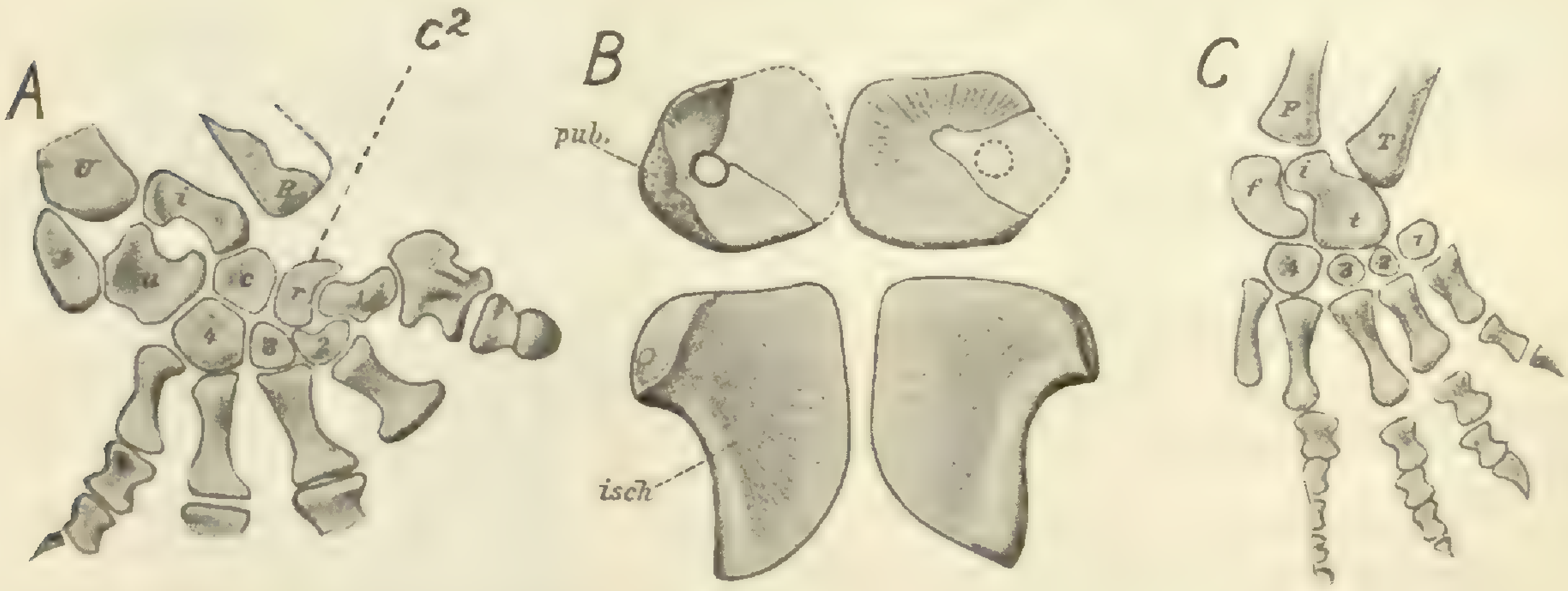
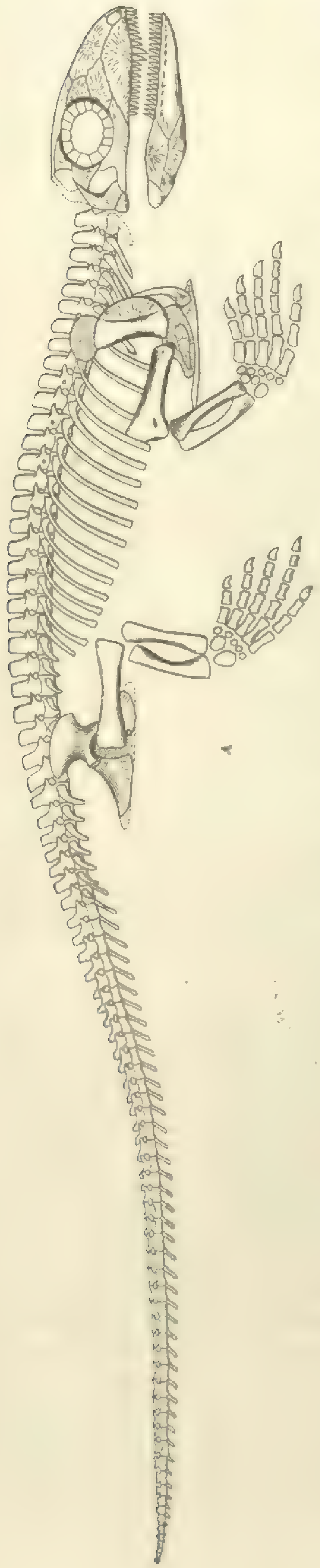


FIG. 8.—The most primitive known Diapsidan. *A*, manus, *B*, pubis and ischium, and *C*, pes, of *Procolophon trigoniceps* Owen (Order PROCOLOPHONIA). After Broom. × ½.

already well separated in the Permian and have been collectively grouped in the superorder Diaptosauria by Osborn. The *second*, or later radiation of the Diapsida, partly sprung from terminal branches of the first, is known in the Triassic, and includes the great orders Parasuchia, Ichthyopterygia, Crocodilia, the superorder Dinosauria, the superorder Squamata, and finally the Pterosauria.

I. *Superorder* Diaptosauria Osborn.



This superorder embraces the Rhynchocephalia of Günther, the Pelycosauria of Cope, which certainly represent distinct orders of reptiles, and the more or less distinct orders or suborders Protorosauria, Procolophonia, Proganosauria, Choristodera, Gnathodontia, Rhynchocephalia. They have appropriately been termed 'rhynchocephaloid' reptiles by Broom.

The common characters of these primitive or stem Diapsida, are as follows: cranium with two complete temporal arches; vertebræ typically amphicœlous and often perforated by a notochordal canal; hypocentra frequently present throughout vertebral column; ribs on all vertebræ from first cervical to eighth caudal inclusive, generally single-headed or incipiently two-headed; large abdominal ribs or plastron always present; coracoid and procoracoid early uniting into a single bone; pubis and ischium ventrally in continuous contact or secondarily fenestrated.

The adaptive radiation of these mostly small sized animals into ambulatory, littoral, amphibious, and fully aquatic types, together with specializations of the skull and dentition for a great variety of feeding habits has resulted in a divergence sufficiently profound and ancient to form seven groups which have been variously assigned the rank of orders or suborders as follows:

Fig 9.—A primitive diapsidan. *Palæohatteria longicaudata.* Restoration by J. H. McGregor. × ¼. Order Protocosauria.

1. *Order* PROCOLOPHONIA Seeley.

This includes the most primitive of the Diaptosauria; those closest to the Cotylosauria, and distinguished by the entire absence of lateroemporal fenestræ,[1] by the persistence of the epiotics and auditory notch of the cotylosaurs, and other very primitive characters. These animals are thus far recognized in the Permian of South Africa only.

2. *Order* PROTOROSAURIA Seeley.

This land group includes Protorosaurus, Palæohatteria, Kadaliosaurus, distinctively ambulatory and in part leaping reptiles, certainly carnivorous; distinguished by the straight limbs, strong development of the hind limbs, correlated with a dorsally expanded ilium and from two to three sacral vertebræ.

These animals show all the characters which we should expect to find in the ancestors of carnivorous Dinosauria; the three genera known are too far specialized in the direction of ambulatory and predatory types to have given rise to any of the other known Diaptosauria.

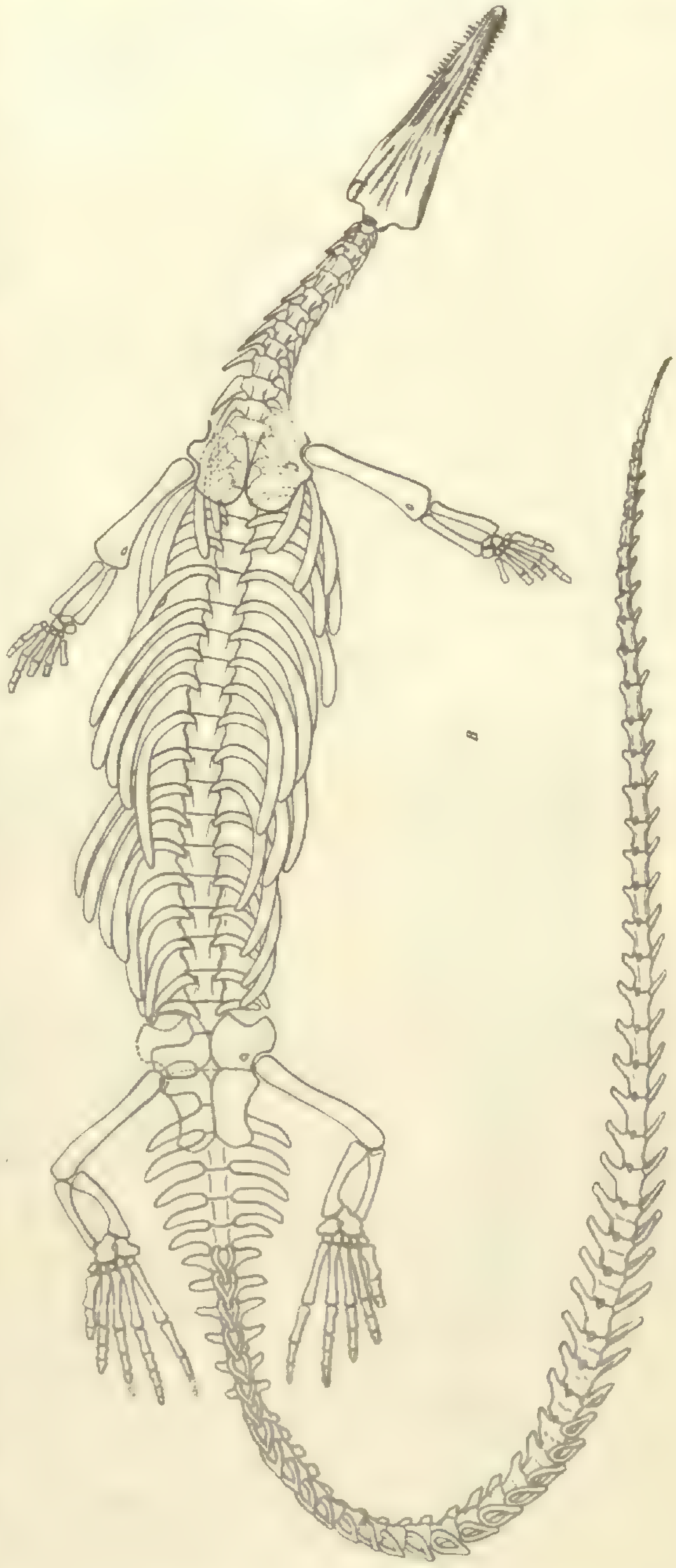


FIG. 10. *Stereosternum tumidum.* Restoration by J. H. McGregor. × ½. Order PROGANOSAURIA.

[1] Dr. R. Broom has just made this important observation.

3. *Order* Proganosauria Baur.

This aquatic or amphibious group, which has been confused with the Protorosauria, is at present represented only by the genera Mesosaurus Seeley and Stereosternum Cope, closely allied forms from the Permian of South Africa and South

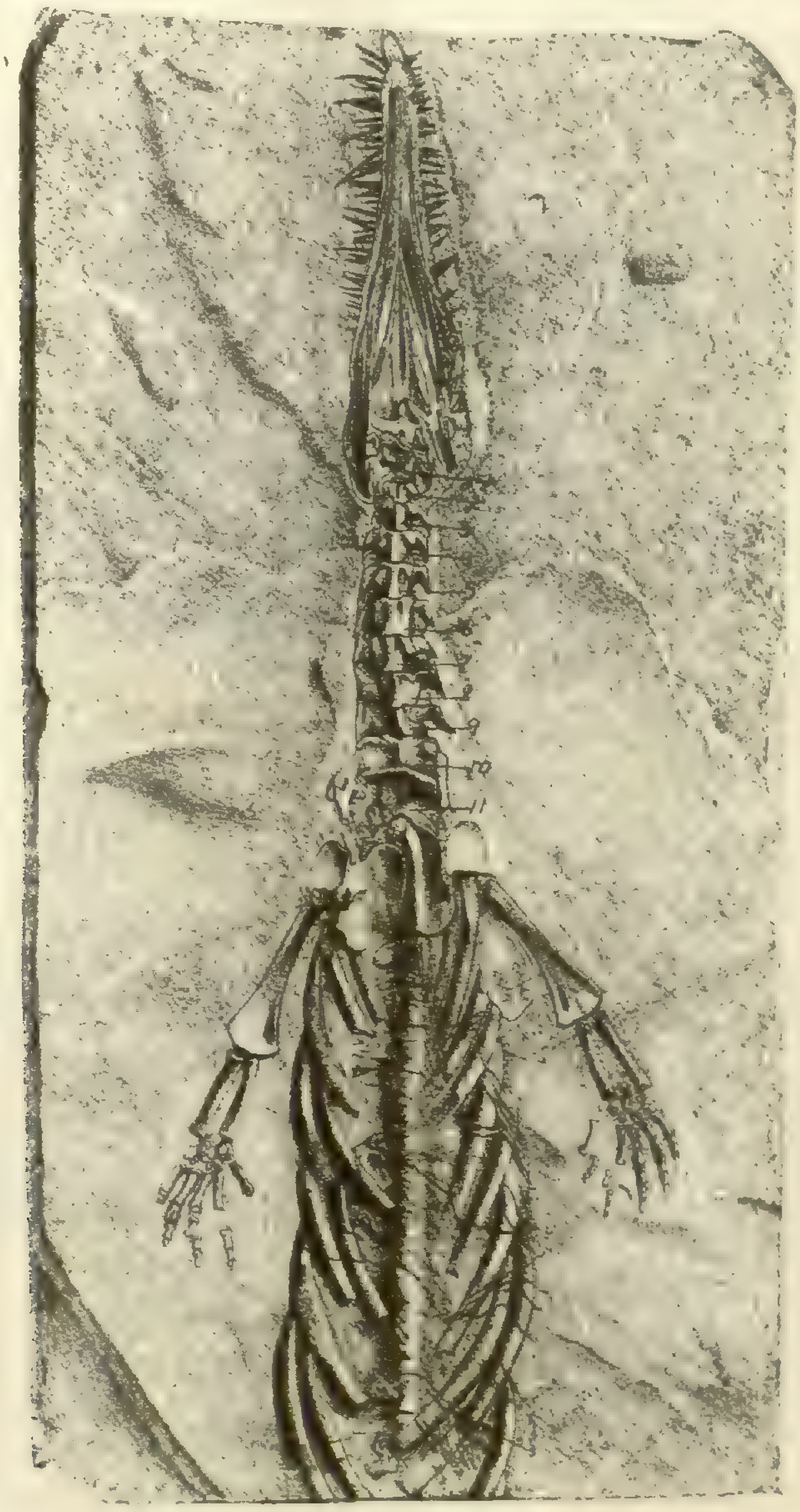


Fig. 10a.—*Mesosaurus tenuidens*. After Gervais. × ½. Order Proganosauria.

America. These are typical swimming or amphibious types, with greatly elongated rostrum, delicate, prehensile teeth, very heavy ribs with highly modified capitular attachments; the vertebræ are also highly distinctive and unique in structure.

These forms also are too specialized to give rise to any of the higher Diapsida; they represent an isolated and dying out group.

4. *Order* GNATHODONTIA Owen.

Rhynchosauria Osborn.

Owen first proposed the "family" Gnathodontia in 1859, typified by Rhynchosaurus, at the same time that he proposed the "family" Dicynodontia. It seems proper that this term should be given priority over the order Rhynchosauria proposed by Osborn in 1903.

Here again we have a highly specialized division resembling the Procolophonia in general body and cranial form, but differing from these animals widely in the concentration of pavement-like teeth on the pterygopalatines and the development of a large edentulous bony beak. They were probably littoral, shell-eating animals far removed from the true Rhynchocephalia.

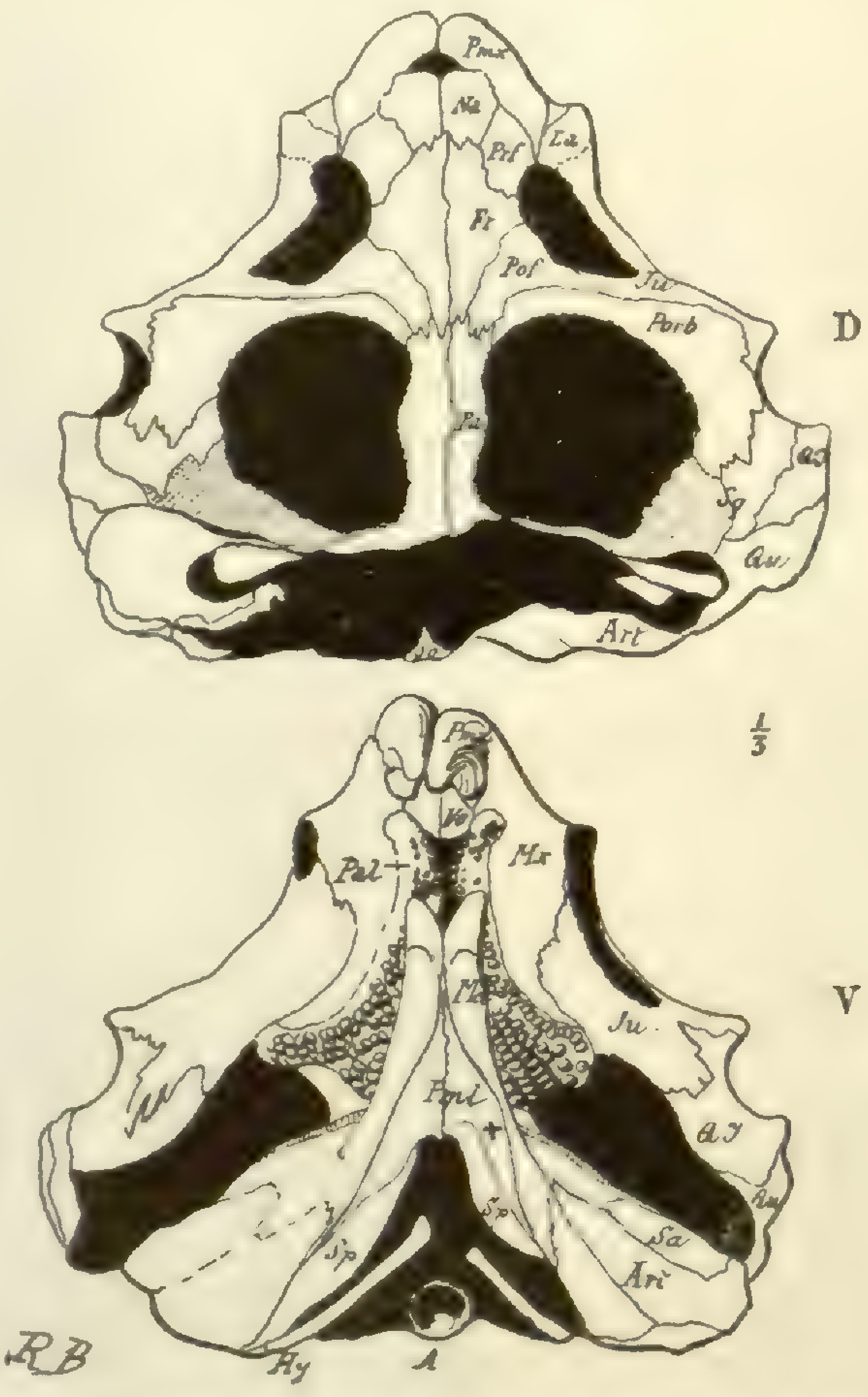


FIG. 11.—Skull of *Hyperodapedon gordoni*. *D*, dorsal, *V*, ventral aspect, × ⅓. After Burckhardt. The black areas represent parts still covered by matrix. Order GNATHODONTIA.

5. *Order* PELYCOSAURIA Cope.

This land group, developed in the Permian of Texas and Bohemia, is distinctively ambulatory and carnivorous. It is characterized by the abbreviation of the tail, the enormous development of the spines of the dorsal vertebræ, also by the

the persistence in certain forms of a suture between the coracoid and procoracoid.

This line also became very highly specialized, and died out in the Trias.

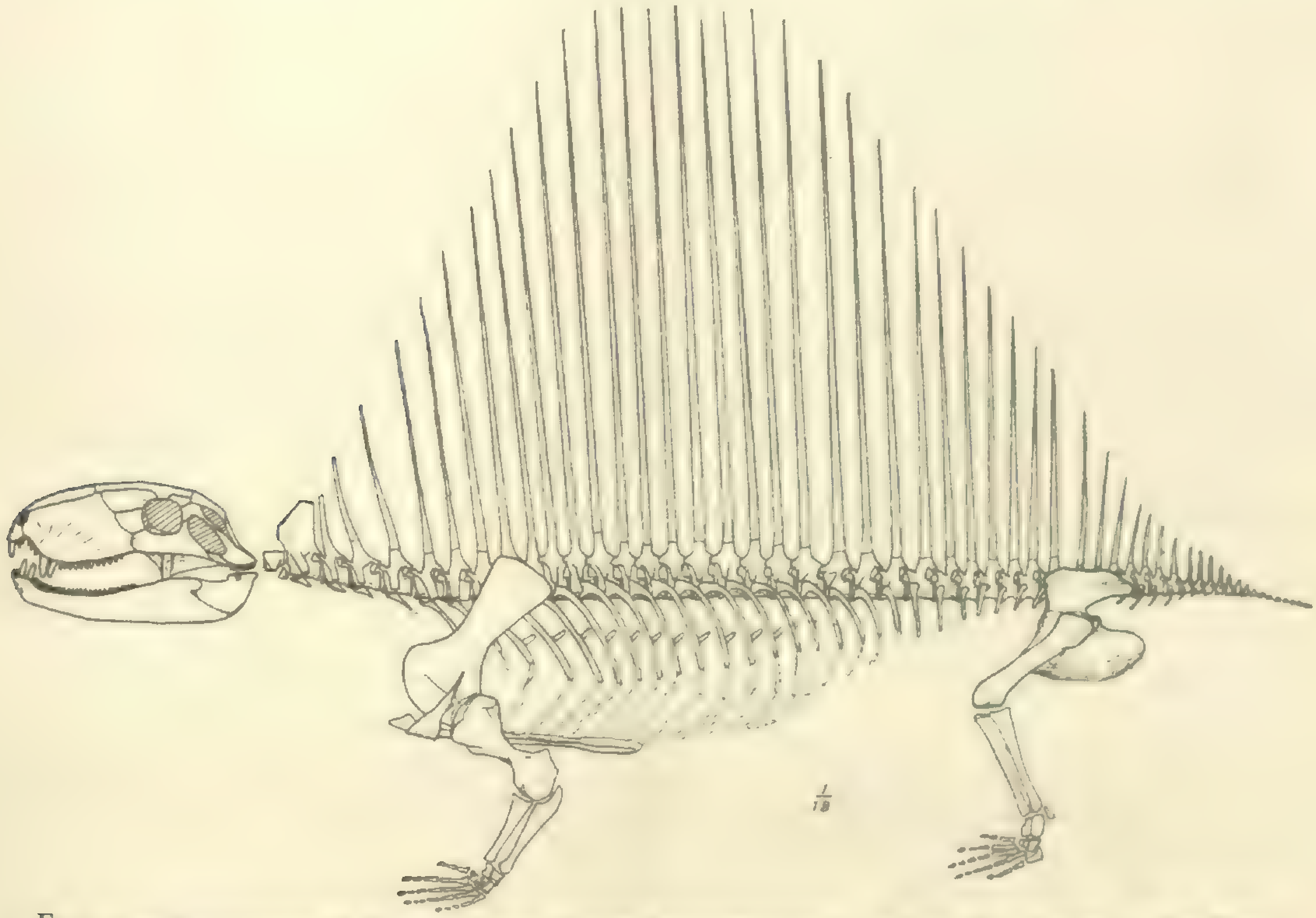


FIG. 12.—Restoration of Embolophorus (Order PELYCOSAURIA). About $\frac{1}{18}$ nat. size. After Case.

6. *Order* CHORISTODERA Cope.

These amphibious animals, found thus far only in the Cretaceous and in the Lower Eocene, represent a sharply defined division with a greatly elongated gavialoid rostrum, teeth acrodont and internally folded, dorsal ribs two-headed. They include the American Champsosaurus and the European Simœdosaurus; the latter being distinguished by more distinct adaptation to aquatic life were made the type of the order Simœdosauria by Dollo. The analogies are with the Proganosauria and the aquatic true Rhynchocephalia, but there are no phylogenetic relationships with these forms.

7. *Order* Rhynchocephalia Günther.

These are the "Rhynchocephalia Vera" of Boulenger. They represent by far the most conservative of all the Diaptosauria because even the recent Sphenodon is in certain respects more primitive than most of its Permian relatives.

The order includes the Jurassic radiation of terrestrial, semi-aquatic, and fully aquatic types, with modifications paralleling

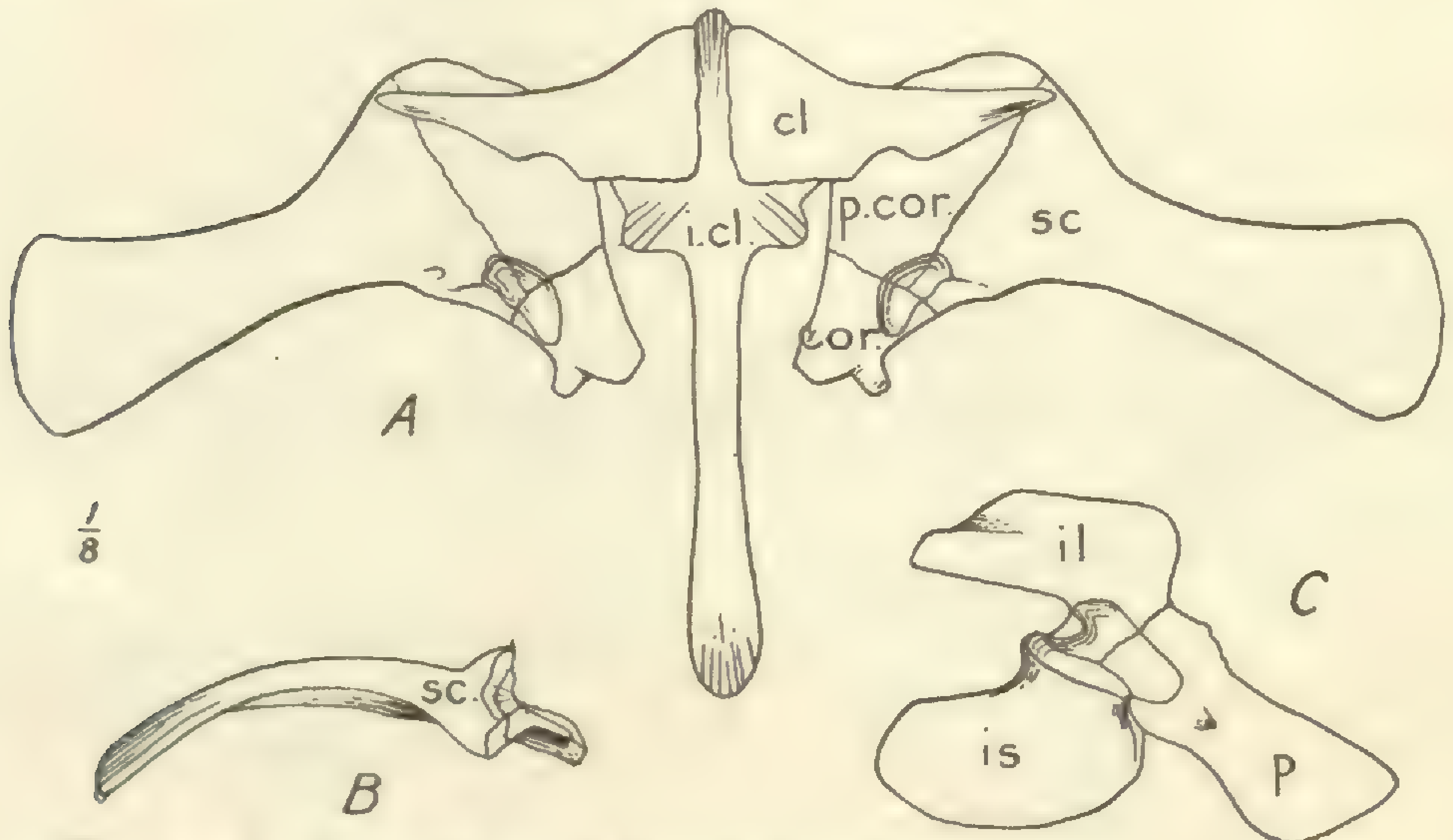


Fig. 13.—*A*. Shoulder-girdle of a Pelycosaurian (Embolophorus) *B*, Profile view of conjoined scapula and procoracoid of same. This is one of the few Diapsida in which the procoracoid is still separated by suture from the coracoid. *C*. Pelvis of same. After Case. × ⅛.

those in the Choristodera and Proganosauria, also the existing terrestrial genus Sphenodon. The Jurassic forms are in many respects less primitive than the existing genus.

II. *Order* Parasuchia Huxley.

This amphibious fresh water group, typified by Phytosaurus and Aëtosaurus, placed in the suborders Aëtosauria and Phytosauria respectively, has long been treated in connection with the Crocodilia, owing to Huxley's influence and authority; McGregor has shown that it has practically no affinity to the Crocodilia, its relationships being closer to the Ichthyosauria, although it constitutes an independent order, probably of freshwater, littoral, carnivorous, short snouted (Aëtosaurus) or long snouted (Phyto-

saurus, Mystriosuchus) forms, analogous in their habits to the modern Crocodilia.

The Parasuchia are found by McGregor to represent an undoubted modification of the rhynchocephaloid or diaptosaurian type.

III. *Order* ICHTHYOSAURIA Blainville.

The ichthyosaurs are also distinctively Diapsida, both in shoulder girdle and in basicranial structure. The latero-temporal fenestra, however, is closed, perhaps secondarily. The posterior position of the nares and the elongation of the snout in front, is analogous to that in the Parasuchia and may be indicative of divergence from a common stem.

The most primitive form, Mixosaurus affords a transition to the ambulatory limb type of the Diaptosauria. None of the known orders of Diaptosauria, however, can as yet be considered ancestral to the ichthyosaurs.

IV. *Order* CROCODILIA Wagler.

We must exclude from the Crocodilia the Parasuchia of Huxley and embrace only the Mesosuchia and Eusuchia of Huxley with the addition of the typical marine forms, the Thalattosuchia, recently monographed by Fraas.

V. *Superorder* DINOSAURIA Owen.

It is a mistake to raise this group to the rank of a subclass, as has been done by some authors, because its three great subdivisions certainly lead back to a common stem form in the Permian which was not dissimilar to the type represented by the Protorosauria.

The ordinal nomenclature still requires further study. At present I am disposed to place the carnivorous forms in the order Theropoda Marsh, including two suborders, (1) Megalosauria for the large types with solid, hour-glass shaped

vertebræ, (2) Symphypoda Cope for the smaller types with hollow, cylindrical vertebræ.

The Opisthocœlia of Owen although proposed as a 'suborder' of Crocodilia appears to enjoy priority of definition over the Cetiosauria of Seeley or the Sauropoda of Marsh.[1]

Similarly the Orthopoda of Cope is distinctively prior to the admirable term Predentata of Marsh. In the selection of these terms we cannot be governed by our preferences; we are bound to stand by the law of priority.

VI. *Superorder* SQUAMATA Oppel.

This superorder ranks in value with the Diaptosauria and Dinosauria inasmuch as it includes the very wide adaptive radiation of three groups of animals which were undoubtedly closely related in origin, namely: (1) Lacertilia, (2) Mosasauria, (3) Ophidia.

The radiation of the Mosasauria from the Lacertilia is analogous to that which we have observed occurring independently in three orders of the Diaptosauria, namely, the Proganosauria, the Choristodera, and the aquatic Rhynchocephalia of the Jurassic.

VII. *Order* PTEROSAURIA Kaup.

There is no question as to the Diapsidan relationships of the Pterosauria and as to their original derivation from Rhynchocephaloid types, although their specialization has carried them to a very great extreme of separation from any known Diaptosauria.

CONCLUSIONS.

I trust that the reclassification of the Reptilia here outlined, and the order of arrangement here adopted will be found to simplify their study. Memoirs now in preparation by Broom on the Procolophonia, by Case on the Pelycosauria, by Brown on

[1] Riggs, E. S. Structure and Relationships of Opisthocœlian Dinosaurs. Part I, Apatosaurus Marsh. *Field Columbian Museum Publ.* No. 82, Aug. 1, 1903.

the Choristodera, by McGregor on the Parasuchia, will further elucidate the still numerous and perplexing questions of phylogeny.

Origin of Aves.—The birds probably originated from a group of Diaptosauria identical with or closely related to that which gave rise to the Dinosauria. It is not true that birds have descended from dinosaurs, but there is very strong evidence that birds and dinosaurs are descended from a common stock.

Origin of Mammals.—There is no question that the mammals are affiliated with the subclass Synapsida rather than with the Diapsida; both in skull and shoulder girdle structure and in the phalangeal formula they are Synapsidan.

As to their nearer relationships they appear to be rather with the superorder Anomodontia and with the order Cynodontia or Theriodontia. The divergence of the mammal stem from these typical reptiles will probably be found to have occurred in the Permian or Lower Trias of South Africa. In fact Broom has recently described what he believes to be a mammal jaw, Karoomys, from the Karoo Beds of South Africa.

American Museum of Natural History,
December 28th, 1903.

THE EARLY DEVELOPMENT OF DESMOGNATHUS FUSCA.[1]

HARRIS HAWTHORNE WILDER.

In a former number of the *American Naturalist* (March, 1899) I presented what seem to have been the only published observations on the development of one of our commonest and most generally distributed salamanders, *Desmognathus fusca*, but as I was then unable to describe the early stages, a most essential gap in this history remained unfilled.

The eggs which furnished the object of my former sketch were laid in the laboratory terrarium on or about June 1, 1898, but as the first observations were made on them June 11, at which time they were in the form of well-formed embryos coiled about enormous yolk-masses, the first eleven days of the development remained unknown, a period which includes the extremely important cleavage stages, the formation of the blastopore and the beginning of the head and tail folds.

Since that time a number of specimens of Desmognathus have been kept in our terrarium each spring, and the favorite hiding-places investigated daily during the egg-laying season, but with no success until the present year (1903) when on June 22 at 1.00 P. M., there was found a batch of twenty freshly laid eggs associated with a small but evidently mature female. At this time the eggs were in the early cleavage stages, and varied from the two-celled stage with the second cleavage forming to that of 16 cells, as represented by the first five rows of Fig. 1. Nine of these were preserved at once in 5% formaline, and the remainder were killed, one or two at a time at intervals representing the most important stages. The eggs were, however, rather few in number, and in spite of considerable conservatism in the daily sacrifice, there were but two left when cleavage was com-

[1] From the Zoological Laboratory of Smith College.

pleted and the blastopore was about to be formed. These two, compelled on June 27 to make a journey with me to Maine, in spite of the utmost care, did not survive the hardships of travel and the experiment came to an end. I am thus able to record the development only during the first three days of existence, leaving the period from the fourth to the eleventh still unknown save through analogy with allied forms, and waiting to be written when occasion may offer.

This early history includes only surface study, mainly of preserved material, but seems to be of especial importance as showing a genuine holoblastic type of cleavage when from the later form of the embryo a meroblastic form was to have been expected.

The various cleavage stages are represented in Fig. 1, in which the first perpendicular column represents them as seen from the upper pole, the second from the side, and the third from below; the figures in each horizontal row representing several views of the same egg. Of these stages the first five occurred simultaneously at the time the eggs were found, 1.00 P. M. June 22, and as no eggs were found the day before, they probably represent stages of 6–15 hours, resulting from eggs laid at intervals during the preceding night.

The successive changes and the descent of the various cells seem evident, and may be traced with an approximate certainty as far as the 23-cell stage, as indicated by the lettering. In the first stage shown, the first cleavage is complete, separating the egg into its two halves, A + B + C + D and E + F + G + H, while the second cleavage, beginning at the upper pole, has proceeded nearly to the equator and is separating the halves into the components A + B, C + D, E + F and G + H, a stage which is seen completed in the second row.

The third cleavage, at least in the eggs examined, is not the typical horizontal one which might be expected, but consists of a set of four meridional ones, which start near the upper pole as so many separate fissures from one of the two former cleavage planes, probably the first. Similar fissures were observed in one instance near the lower pole and it is evident that those from above and those from below meet one another, and result

1st cleavage completed, 2nd cleavage begun, June 22, 1.00 P. M. [The eggs were found at this date, and then presented various stages, from this to that of 16 cells.]

2nd cleavage completed, 4-celled stage. June 22, 1.00 P. M.

Beginning of 3rd cleavage. June 22, 1.00 P. M.

3rd cleavage completed, 8-celled stage. June 22, 1.00 P. M.

4th cleavage completed 16-celled stage. June 22, 1.00 P. M.

28-celled stage, with 16 micromeres, 12 macromeres. June 22, 4.30 P. M.

42-celled stage, with 26 micromeres, 16 macromeres. June 22, 11.00 P. M.

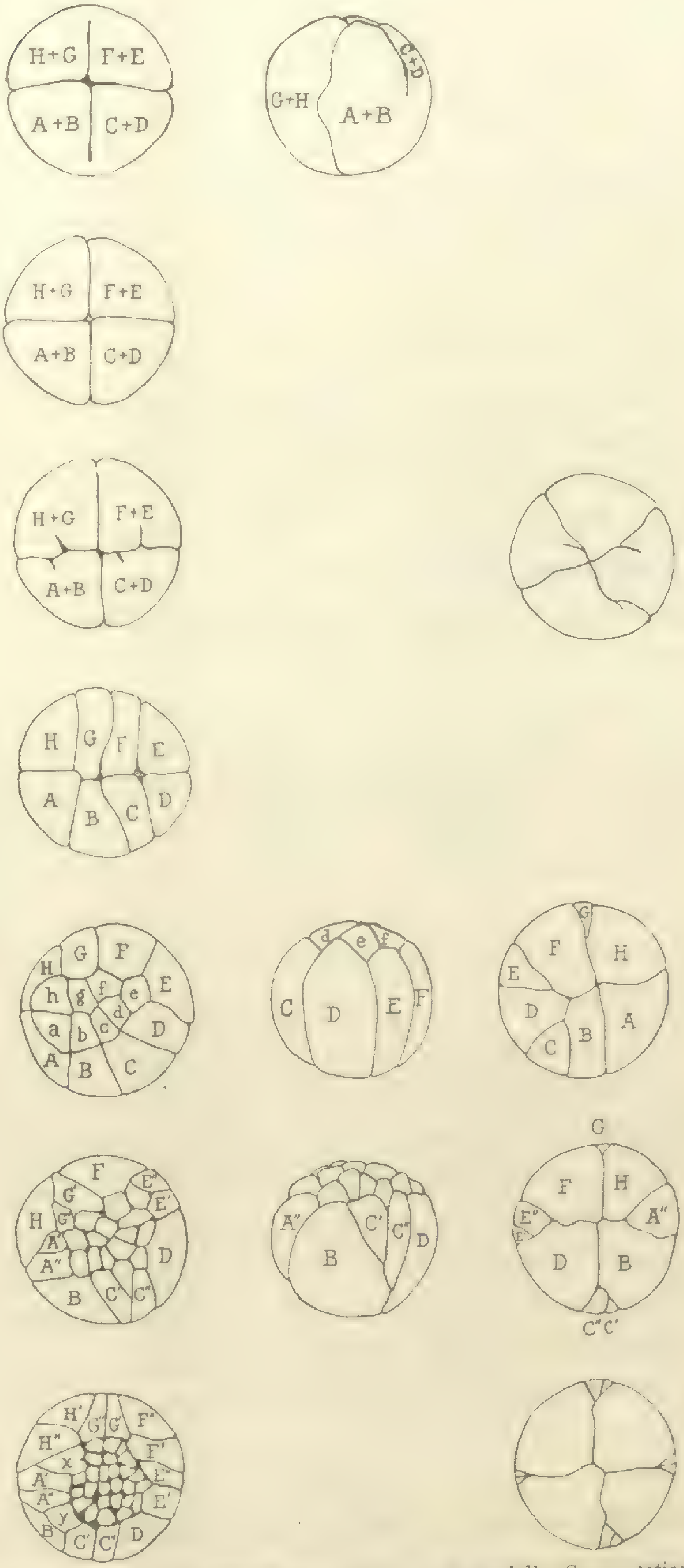


FIG. 1.— Eggs of *Desmognathus fusca* [1903 material]. Segmentation stages, observed June 22, between 1.00 and 11.00 P. M. The left-hand column shows upper poles; the next side views; and the right-hand one, lower poles. × 6.

in the formation of an eight-cell stage, which is bilateral along the plane of the first cleavage, and consists of the four cells A. B. C. and D. upon one side, and of E. F. G. and H. on the other (fourth row of Fig. 1). These eight meridionally arranged blastomeres do not seem to have equal value in respect to size, for through a slight obliquity in these four new lines of cleavage there result four smaller blastomeres which alternate with four larger ones, and of these the latter alone usually attain the lower pole while the former ones do not reach it. This is seen by a study of the lower pole views in the fifth and sixth rows of Fig. 1, where the smaller blastomeres A. C. E. and G. intrude like wedges along the lines of the first two cleavages, but do not reach the pole save in the single instance of A. in the fifth row, an unusual condition.

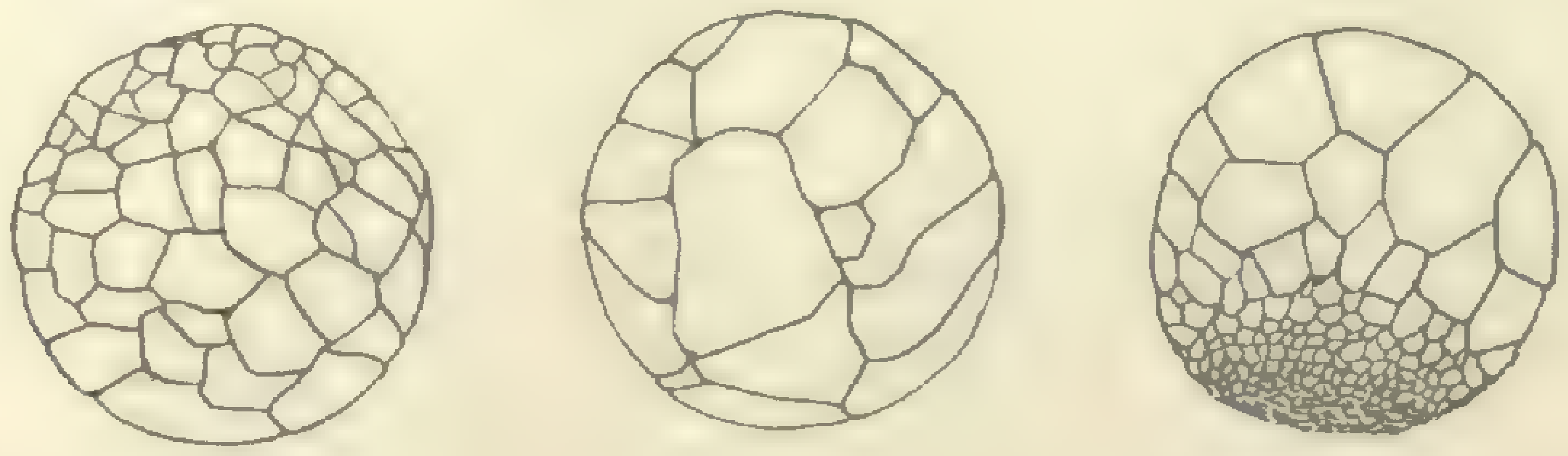
The next cleavage is an horizontal one, forming an approximate circle about the upper pole, and cutting off small segments from each of the eight blastomeres of the preceding stage (fifth row). This results in a 16-cell stage, consisting of eight micromeres, a, b, c, etc., clustered about the upper pole, and eight macromeres, the remaining parts of the original cells. This last cleavage takes place so far above the equator of the egg that it does not change the aspect of the lower half, and thus the drawing of this egg (the third of the fifth row) would answer equally well for the preceding one.

By a comparison with Eycleshymer's studies of Amblystoma, (*Journal of Morphology*, Vol. X, 1895) it becomes evident that this latter cleavage is the one which is described as typically the third in Amphibian eggs, and that the four meridional cleavage lines which result in the formation of the 8 cell stage, together form the usual fourth. Indeed, this transposition of the two cleavages occasionally occurs in Amblystoma, and as my observation rests upon the study of but two eggs, it cannot be asserted that the order described is the typical one in Desmognathus. It is, however, identical with the method shown and figured by Kerr in Lepidosiren, and his figures of the third cleavage (by means of the four short lines) as copied by Ziegler (Figs. 213–314 of his *Entwicklungsges. der niederen Tiere.* 1902) would serve in every respect as better pictures of Des-

mognathus eggs in the corresponding stages than I have been able to draw. The occurrence of the third meridional before the horizontal cleavage seems also to be the rule in Acipenser and in Amia.

The next stage, that of 28 cells, is shown in the sixth row, and appears to consist, first, of a division of each micromere, increasing their number to 16, and, secondly, of a longitudinal division of the smaller macromeres A, C, E, and G, into A′. A.″ C′. C″. etc., while the other four B. D. F. and H. remain undivided. The subdivisions of the smaller macromeres may or may not be visible from the lower pole, as is seen in the third figure of the row.

Beyond this the subdivisions cannot be followed with certainty, but the last figure shown (seventh row of Fig. 1) which consists of 26 micromeres and 16 macromeres, 42 in all, appears in some



June 23, 10.30 A. M. Side view. June 23, 10.30 A. M. Lower Pole. June 24, 11.30. M. Lower Pole.

FIG. 2.— Eggs of *Desmognathus fusca* [1903 material]. Later segmentation stages, representing a direct continuation of the series shown in Fig. 1. × 6.

respects to show some regularity, although in others it is disappointing. We would expect, indeed, to account for the increase from 12 to 16 macromeres by a subdivision of each of the remaining ones, B. D. F. and H, but while this can be seen to be the fact in the case of F and H, the two other new macromeres cannot well be explained by a subdivision of B and D. Instead of this, they appear as those marked x and y, and the relation of those and of B and D to the smaller intruded macromeres is such as not to allow the desired interpretation. Less difficulty appears in the interpretation of the 26 micromeres, for while we would naturally expect a doubling of each of the 16 of the former stage, and a consequent 32 in this, its smaller number may well be accounted for by the supposition that some of the original 16 have not yet divided. No definite interpretation

can be made, however, for this 42-cell stage, since but a single specimen was available for study, but it may be seen from the above sketch of this and the preceding stages that the eggs of Desmognathus will furnish a very interesting and convenient object for the study of cleavage problems in Amphibia.

Sketches of two later cleavage stages are given in Fig. 2 and may be seen to consist of a greater and greater subdivision of both micro- and macromeres, apparently without special regularity. The last figure (June 24) represents the lower pole of the oldest stage I succeeded in obtaining.

The above observations, which establish the fact that the

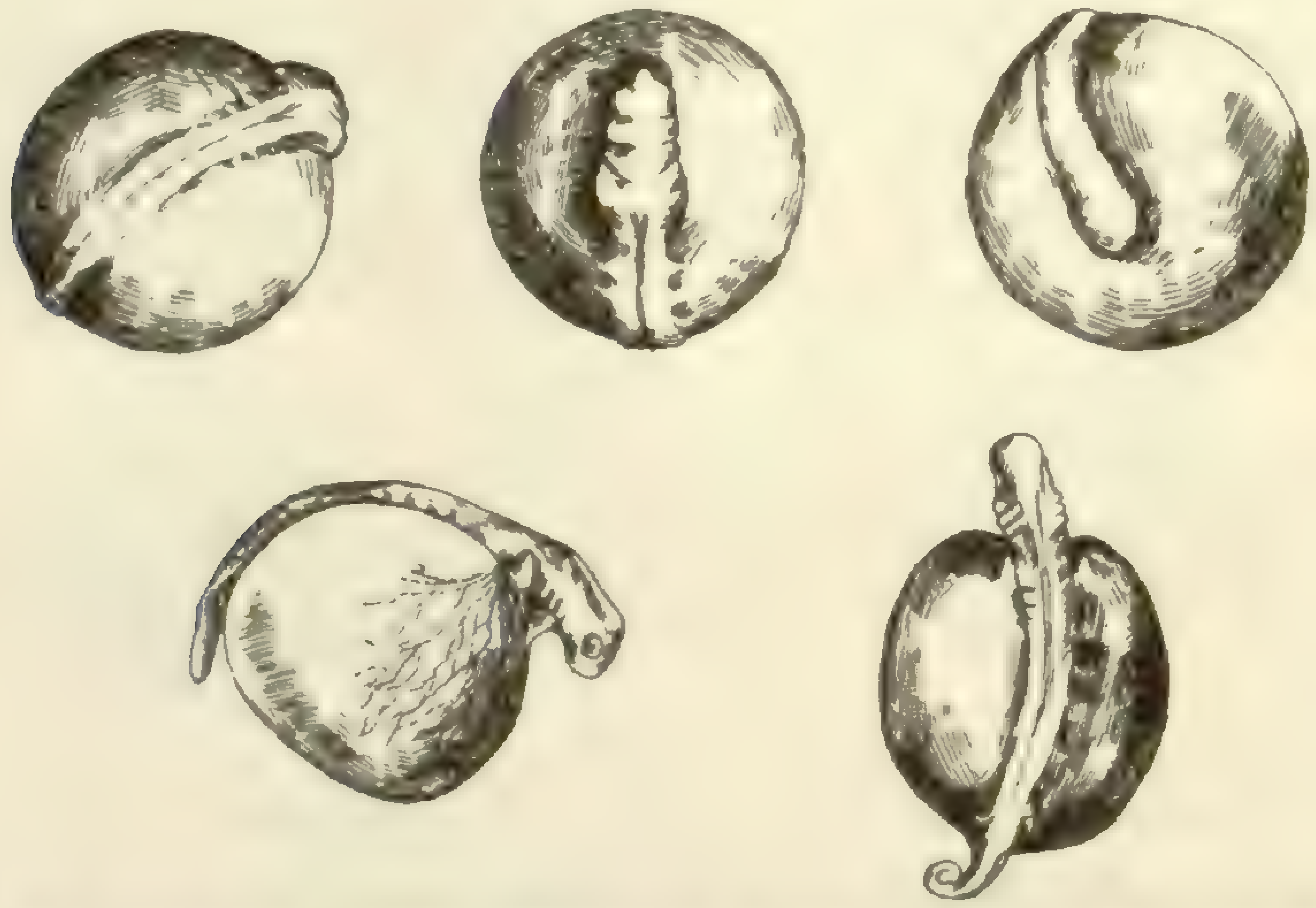


FIG. 3.— Early embryos of *Desmognathus fusca* [1898 material]. The figures in the upper row represent different aspects of a single egg of the stage described in the previous paper as "A." Similarly, the two figures of the lower row represent different aspects of the stage described primarily as "B." × 6.

eggs of Desmognathus are holoblastic, will serve to correct the statement to the opposite effect given in my previous article on the subject, and while it is always unpleasant to be proven in a mis-statement, it is more satisfactory to the investigator to be able to furnish his own proof than to leave it to others. At the time of writing my previous article, I possessed no embryos younger than those represented in the upper row of Fig. 3, and it then appeared to me impossible that such a relation between embryo and yolk as the one shown here could result from an egg of the holoblastic type. A slightly older stage, that represented in the second row of Fig. 3, seemed still more convincing in this respect, since by this time a set of branching blood vessels

had made their appearance on the surface of the yolk, reminding one forcibly of similar embryos *e. g.*, those of certain Teleosts, that result from meroblastic eggs. Too sharp a distinction between the holoblastic and meroblastic type cannot, however, be drawn, since there are numerous transition forms, as that of *Salamandra maculosa*, in which the egg is 4–5 mm. in diameter, and the first two cleavage planes, although they slowly cut their way around the egg on the outside, often fail to divide the yolk internally, "so dass die Furchung in den ersten Stadien partiell ist" (Ziegler *loc. cit.*, p. 249, on the authority of Grönroos, 1903). A similar condition has been produced experimentally in the frog's egg by O. Hertwig (1897). The eggs of the Gymnophiona, which are the largest of all Amphibian eggs, (7–8 mm. in *Hypogeophis rostratus*) are at first typically meroblastic, with a germinal disk that spreads gradually over the yolk; but during and after gastrulation the yolk becomes divided up into large cells, so that the eggs are ultimately holoblastic.

In these latter, also, as well as in the eggs of Salamandra and Desmognathus, there is a noticeable array of blood vessels upon the yolk, which at first sight closely resembles a true yolk circulation, but which in reality consists of the vessels which normally appear superficially in the region distended by the yolk mass, and thus, although they may receive nutriment from the yolk, they are in no sense true vitelline vessels. The veins of this region, though not the arteries, could be closely followed in the two series from which Figs. 4 and 5 were taken, and are shown to be three in number, one median and two lateral. The median vein lies along the mid-ventral line of the swollen abdomen, scarcely noticeable posteriorly, but increasing anteriorly as it picks up several lateral branches. It passes along the dorsal (concave) aspect of the liver and enters the sinus venosus in company with the hepatic vein. By its position and course it undoubtedly corresponds to the abdominal vein of the adult, and thus, although it may be also a potential portal, it cannot be very definitely related to the true vitelline veins of meroblastic embryos. In the same way the two lateral veins are seen to be identical with the large cutaneous veins which lie along the sides

of the trunk. They empty into the *Ductus cuvieri* near the entrance of the subclavian.

Thus, although it is seen that many Amphibian eggs are on the border between the holoblastic and meroblastic types, and although they form interesting transitions between the two, especially useful in breaking down artificial distinctions, yet it must be confessed that through the observations here recorded the eggs of Desmognathus are at first almost typically holoblastic, although in the later relation of embryo to yolk they greatly resemble meroblastic embryos. (*cf.* Fig. 3 of this paper with the following in Ziegler's text-book, 1902, Fig. 304.) Hypogeophis (Brauer); Fig. 188 herring (Kupffer).

In concluding this paper I wish to present a few sections

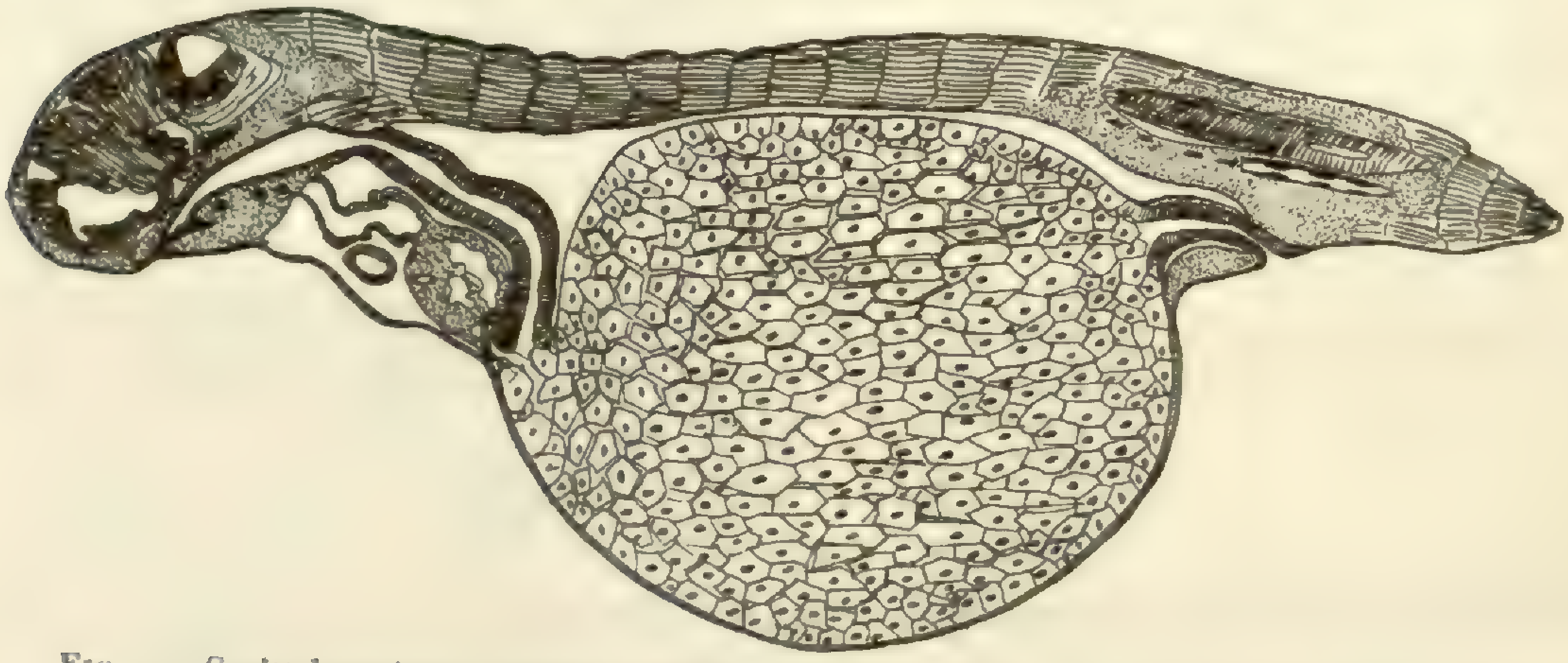


Fig. 4.—Sagittal section, a little to one side of the median line, of an advanced embryo of *Desmognathus fusca* [1898 material] a little older than "Stage D" of the previous paper. × 15.

taken through advanced embryos of Desmognathus (the 1898 material) which will show the actual relation of the embryo to the large yolk mass and will demonstrate its cellular character in the later stages.

Fig. 4 is a sagittal section of an advanced embryo, and shows the median relationships in the ventral half, but strikes the brain and the dorsal portion somewhat laterally. By combining several adjacent sections, the pharynx, œsophagus and anus were completed. In this the peritoneum may be followed dorsally as a continuous line investing the rectum, the yolk mass and the œsophagus, and enclosing a portion of the cœlom; and ventrally around the yolk mass enclosing a large cœlomic space

ventral to heart and liver and a smaller one ventral to the anus. The entire yolk mass, which is wholly cellular, is enclosed within the peritoneum and is morphologically the equivalent of the middle portion of the intestinal tract in which a lumen has not as yet appeared. Fig. 5 shows four cross-sections of an embryo a little older than that of Fig. 4 and taken from a single series, the first through the liver, the second through the yolk at its greatest circumference, the third through the hip-girdle and rectum and the fourth through the cloaca, with the hind-limbs at the side. The numbers attached to each are those of the sections as numbered in the series. These show the same relationships as seen in Fig. 4, the second especially, in which two lateral

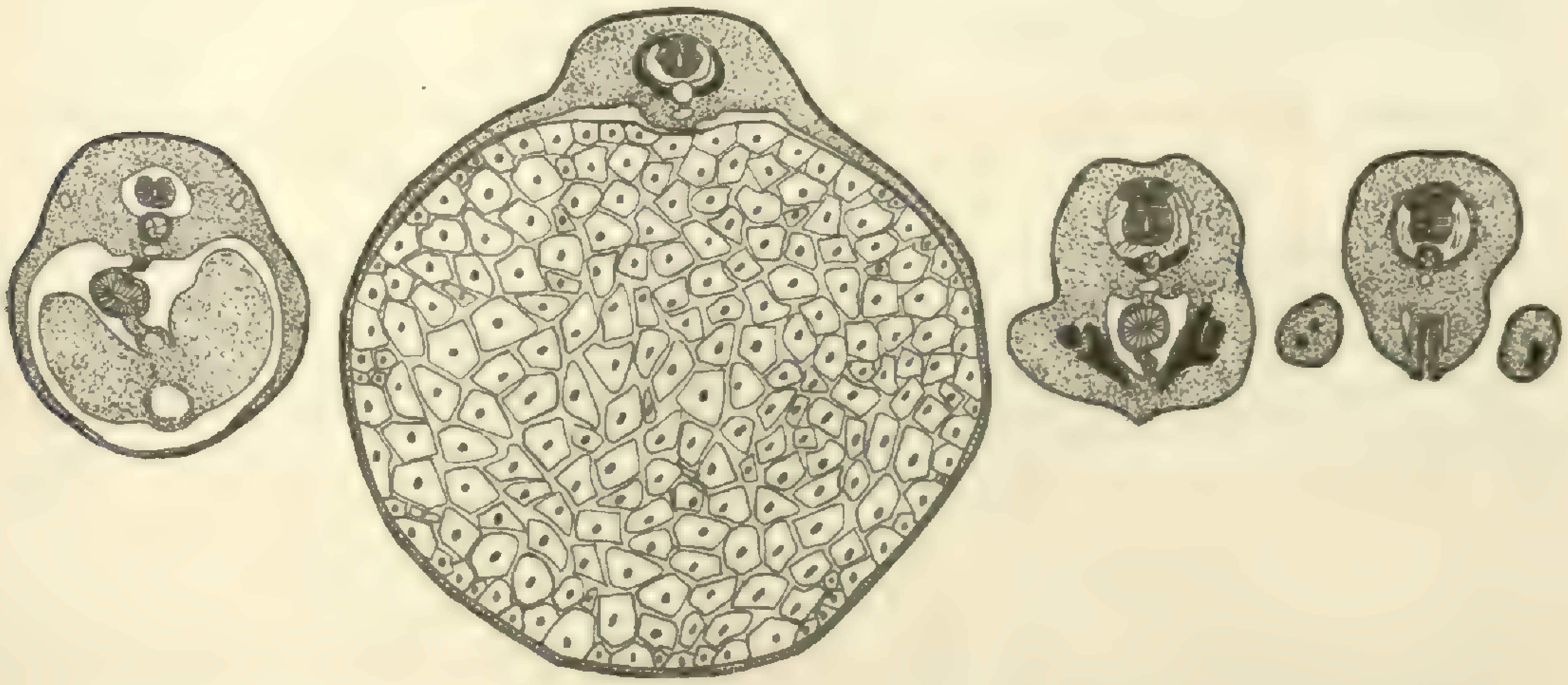


FIG. 5.—Four cross-sections from an advanced embryo of *Desmognathus fusca* [1898 material] slightly older than Fig. 4. The sections are 20 μ in thickness, and the complete series, from the tip of the nose to the end of the cloaca consists of 335 sections. The numbers affixed to the sections in the figure indicate their place in the series. × 15.

cœlomic spaces may be seen dorsal to the yolk-mass, separated by a mesentery. In the first the alimentary canal (œsophagus or beginning of stomach) is suspended between dorsal and ventral mesenteries, in the latter of which lies the already well-developed liver, while in the former is seen the beginning of a pancreas. In the third section are seen the two lateral cœlomic cavities, dorsal and ventral mesenteries, the hip girdles and the heads of the femora, and in the fourth are the last (most posterior) remnants of the cœloms, the open cloaca, and the two legs, the one cut through the femur, and the other through tibia and fibula.

SMITH COLLEGE,
Nov., 1903.

THE HISTOLOGY OF THE LIGHT ORGANS OF PHOTINUS MARGINELLUS.[1]

ANNE B. TOWNSEND.

ORGANIC light has always been a subject of interest, both to the scientist and to the casual observer of nature, and no other photogenic organisms are of such wide range and easy access as the fireflies. In some of its phases the light of the firefly comes within the scope of the physicist and chemist. To the former belongs the consideration of its nature, of its spectrum and other physical properties ; to the latter come the problems of chemical analysis concerned with the phenomenon, but to the student of entomology remains the study of the delicate living structure in which this wonderful process of photogeny takes place.

In spite of the abundance of these insects, little work has been done on the structure of the light-organs in our American fireflies. During the past twenty years some careful investigations have been made upon European and Cuban forms, but there is practically no literature upon those of our own country. The purpose of my study has been to learn something of the histology of the light-organs of *Photinus marginellus*, the most common firefly about Ithaca during June and July This work was begun at the suggestion of Dr. Wm. H. Seaman of Washington, D. C., whose advice during its progress has been most helpful. I am also indebted to Professor Comstock and to the members of his staff at Cornell University for their kindly supervision of my work.

The material from which this work was done was collected near Cornell University during the summers of 1901 and 1902. The insects begin to appear by the middle of June, but are not abundant until July. The height of the flying season is during the first part of July. The large majority of the insects

[1] Contribution from the Entomological Laboratory of Cornell University.

caught were males. A number of females were found, but never on the wing. They were always either in the grass, or on some low plant where they could easily have climbed.

Three methods of fixation were tried the first summer. For two of these the insects were killed by dropping into hot water. The caudal part of the abdomen was then clipped off and put into the fixing fluid without removing any part of the chitin. Half of this material was fixed for twenty-four hours in Flemming's solution (strong). This proved almost worthless, with the exception of a single slide. The other half of this material was fixed in Gilson's mercuro-nitric solution for seven hours. This gave very good preparations of the general features of both layers of the light-organs.

The third lot of material was killed and fixed in hot 70% alcohol. This was satisfactory for the gross structure of the organs, though not good for the finer details.

The second summer the killing of the insects in hot water was abandoned. The cadual portion of the abdomen was clipped off, the tip cut away, and the dorsal wall removed to insure better penetration of the fixing fluid. The living tissue was then put directly into the fixer. Flemming's fluid, after this treatment, gave much better results than before. Hermann's fluid gave a fairly good fixation. The cells of the cylinders are definitely outlined in these preparations, but the tissues in general are opaque.

By far the best results for the tracheal structures were obtained by the use of osmic acid. The strength of the acid was varied from .1% to 1%, and the time of fixation, from two to thirty hours. The best preparations were from material left for thirty hours in 1% osmic acid.

Material fixed in Flemming's or Hermann's fluid, or in osmic acid, was washed for twenty-four hours in running water. That fixed in Gilson's fluid was put directly into 70% alcohol. All the material was dehydrated by carrying it through the grades of alcohol, from 70% to absolute. Cedar oil was used for clearing. These sections were all cut in paraffin.

The greater part of the sections were cut 10 μ in thickness, but a few thinner sections, 3 μ and 5 μ, were made for the determination of some finer structural points.

The material was all stained after the sections were cut. The Gilson and alcoholic sections were stained for about two minutes in Gage's chloral hematoxylin, and for a half minute in eosin. This gave satisfactory general results. A double stain with alum carmine and picric acid did not prove a good stain after Gilson's fluid. Following fixation with osmic acid, Hermann's or Flemming's fluids, safranin proved most satisfactory. The sections were stained for twenty-four hours in a mixture of equal parts of saturated aqueous and alcoholic solutions of safranin, then differentiated in absolute or even slightly acid alcohol. Iron hematoxylin is also a good stain for osmic acid material.

Carbol-xylene was used as a clearer, and the sections were mounted in Canada balsam.

Teazed preparations were made by dissecting out the light-organs entire, placing them for from fifteen to thirty minutes in ·5% osmic acid, then for a few minutes in weak caustic potash, and teazing in normal salt solution.

Experiments with methylene blue injection were not successful. Only one insect showed any coloration of the central nervous system, and in that the finer nerves could not be traced. It is difficult to get a good injection with such small insects. However, my attempts in this line were begun near the close of the collecting season, and with further experimenting it is possible the results might have been better. The most successful specimen was killed an hour and a half after injection.

Since the old idea that the firefly's light was dependent upon the presence of phosphorus or some similar substance has been abandoned, other theories have been advanced in attempt to explain the phenomenon. The view generally accepted is that the light results from the oxidation of a substance produced by the metabolism of the light-organ cells. The nature of this substance has not been determined, but that its photogenic property is independent of the life of the cell is proved by the fact that when the organs are dried and reduced to a powder the light reappears under the influence of air and moisture. When the fresh photogenic tissue is crushed, the light increases in brilliancy, and it is some time before it wholly disappears. Radziszewski ('80) through his study of the artificial luminosity

of lophin, discovered a series of carbon compounds similar to those found in living organisms and capable of becoming luminous under conditions compatible with life. The conditions necessary for this production of light he found to be the presence of oxygen, an alkaline reaction and slow chemical action. Watasé ('96) states that in the firefly the phenomenon is due to the oxidation, in alkaline media, of a granular substance secreted by the cells of the photogenic tissue. He offers no further suggestion as to the character of the substance than that it is "a secretion of fatty nature." He gives as proof of the oxidation theory the fact that when the photogenic material is crushed on a slide and lowered into a jar of carbon dioxide the light disappears instantly, but reappears when the slide is placed in a jar of oxygen, or simply in the air. This may be repeated several times with the same material. Watasé recognizes the necessity of moisture as well as of oxygen in the process of photogeny.

Dubois stands almost alone in opposing the theory of oxidation. As a result of experiments with ozone, nascent oxygen and oxygenated water he states ('95), that the action of energetic oxidizing reagents at once and finally extinguishes the light, without first causing any increase in brilliancy. However, the absence of oxygen seems to destroy the light, as it is suspended when the light-organs are placed in a vacuum. From his earlier work he concluded that the light was the result of a process of crystallization. His later work ('98[a]) has led him to abandon this theory. He still rejects the oxidation hypothesis as crude and unscientific, and offers in its place one of a reaction between two substances to which he has given the names luciferase and luciferine. The accessibility of the material led him to use *Pholas dactylus*, a marine mollusk, as the basis of his study. The inner wall of the siphon of a large Pholas was scraped with a knife and the resulting pulp crushed with sand and 95% alcohol. After twelve hours it was filtered and a liquid obtained which was not luminous, even after vigorous agitation with air. The alcohol was drained off from the residue and chloroform added. After some hours a second non-luminous liquid was filtered off. A mixture of one part of the first liquid with three parts of the second gave a beautiful

luminescence at ordinary temperature. By adding to liquid No. 2 five or six times its volume of 95% alcohol, or by boiling it, a white floccose precipitate was formed and the mixture of the remaining liquid with liquid No. 1 no longer produced light. He therefore considers the white precipitate as constituting one of the two photogenic substances, the luciferase. Luciferine was obtained in an impure state by evaporation of alcoholic liquid No. 1. Another experiment was tried with the luminous mucous secreted by Pholas. Two portions of the mucous mixed with water were taken, and one extinguished by agitation, the other by bringing to the boiling point. The mixture of the resulting non-luminous liquids was photogenic. A similar result was obtained with the prothoracic organs of *Pyrophorus noctilucus*. One was extinguished by crushing, the other by dropping it into boiling water. When the latter was crushed and mixed with the former, the light reappeared.

Dubois therefore states that he has established experimentally that the light of living organisms is produced, in the presence of water and oxygen, by the reaction between luciferase, an instable proteid substance possessing in large measure the general properties of an enzyme, and luciferine, a chemical substance. While Dubois confidently asserts that biological light is not a result of oxidation, his experiments would not seem to prove this conclusively. He himself admits the necessity of oxygen, and even if the process is not one of simple, complete oxidation, it would yet seem probable that oxidation is the essential factor in photogeny.

The photogenic tissue of Photinus responds definitely to the action of oxygen. A series of experiments shows uniformly a decided increase in the brilliancy of the light when the tissue is placed in a jar of oxygen. Tissue in which the light has been wholly extinguished by the action of carbon dioxide becomes instantly photogenic when placed in oxygen. Until there has been more extensive experimental study of a large number of organisms, generalizations on the subject of organic light are unsafe.

The fact that Dubois's work was done upon a marine organism is significant. If, as one must assume, the photogenic function

has arisen independently in different organisms, it would not seem strange that the light of such widely separated forms as a marine mollusk and a terrestrial insect, though in both cases a process of oxidation, might be produced in a different manner.

The physical properties of the firefly's light have been studied by Dubois, Langley and Very, Young, and Watasé, with essentially the same results. The spectrum given by the light of the Lampyridæ is perfectly continuous, without any trace of lines, either bright or dark. It lies within that portion of the spectrum which most powerfully affects the organs of vision, though having small thermal or actinic effect. Dubois has demonstrated by photography the presence of some actinic rays in the light of Pyrophorus. A single insect was used, and five minutes was required for printing from a plate which would have taken only a fraction of a second with sunlight. Dubois attributed the presence of actinic rays to a fluorescent substance which he found in the blood.

Most careful and elaborate experiments have failed to show more than an infinitesimal amount of heat connected with the light. One authority even goes so far as to say that not more than one-thousandth of the energy expended in the flash of the firefly is converted into heat waves. When one considers that in our ordinary oil or gas lamps more than ninety-nine per cent of the energy is lost as regards illumination, and that even in the arc light only about ten per cent. of the waves are visible, the interest which this "cheapest form of light" arouses from the economic point of view is very apparent. It is also an alluring problem to the student of physics to determine by what process the medium wave lengths are produced independent of the longer and shorter waves. If this "secret process" could be wrested from nature, its economic value would prove almost inestimable.

While the phenomena of biological light early attracted the attention of observers of nature, as Aristotle, Democritus and the naturalist Pliny, it is only within the last century that any serious study has been given to the organs which produce it. The discovery of their cellular nature may be credited to Peters. In 1841 he refuted the theory of Carrara ('36) that the light was dependent upon an air-sac extending from the mouth to the light-

organs and acting as a bellows, and stated that the photogenic tissue was made up of little spheres, regularly arranged and penetrated by the tracheæ. Leydig and Kölliker in 1857 definitely recognized the cellular structure of the light-organs. Their work has been followed by that of several other European investigators During the past twenty years Wielowiejski and Emery have made important histological researches upon species of Lampyris and Luciola.

All recent workers agree in stating that the ventral light-plates of the male lampyrids are composed of two more or less clearly defined layers; the dorsal, chalky, opaque layer, and the ventral, or truly photogenic layer. The former is composed of fairly regular, polygonal cells, filled with a great quantity of crystals of urate salts. The ventral layer is composed of two distinct elements; the tracheal structures and intermediate areas of parenchyma. The parenchyma cells contain fine granules of non-urate composition. The main tracheæ of the photogenic segments send vertical branches down through the light-organs. Aside from their profuse branching they show no unusual features until they reach the ventral layer. The tracheal structures within the ventral layer differ in different forms, and the two species upon which Wielowiejski and Emery based the bulk of their work, *Lampyris splendidula* and *Luciola italica* respectively, show a considerable difference in this respect. In Luciola each vertical tracheal axis is surrounded by a cylindrical mass of semi-transparent tissue, within which it branches in an arborescent manner. The method of branching in Lampyris is fasciculate, rather than aborescent, and the tracheæ are much less regular in their distribution. Max Schultze, in 1864, found in osmic acid preparations from the light-organs of *Lampyris splendidula* certain blackened bodies at the periphery of the cylinder. These he found to be penetrated by the finer tracheæ. Failing to find further continuations of the tracheæ beyond these bodies, he called them the "tracheal end cells." Wielowiejski ('82), in his study of the same species, found that instead of having their ultimate endings within the so-called "end cells," the tracheæ branch, sending out fine "tracheal capillaries" which extend beyond the cylinder and in most cases anastomose with those of

adjoining cylinders. Emery, from his work on Luciola, confirms the views of Wielowiejski in all points except as regards the anastomosing of the capillaries. He found them always ending free, never uniting with those from the same or another cylinder.

In this work the nomenclature previously used has been retained except in a few cases where a change seemed especially advisable. The more familiar terms phosphorescent and luminescent, with their nouns, are abandoned and photogenic and photogeny substituted. Phosphorescent is objectionable as it suggests that the light is due to the presence of phosphorus. Photogenic — light-generating — gives a more definite idea of the actual phenomenon than luminescent. The name "end cells" was used by Max Schultze because he believed the tracheæ had their ultimate endings within these cells. Now that it is proved that the tracheæ do not so end, but merely pass over into the tracheolar network, the name "transition cells," as used by Holmgren ('96), is far preferable. The term tracheoles, which is used elsewhere in insect histology to designate fine trachael branches not possessing spiral thickening, is preferable to "tracheal capillaries."

The light-organs of the male of *Photinus marginellus* are in the form of two plates lying above the ventral body wall of the fifth and sixth abdominal segments. (Figs. 1 and 2.) The underlying cuticle is transparent, allowing free emission of the light. The plates lie just beneath the central nervous system and directly upon the very thin hypodermis. They are yellowish white in color. In the female of the same species there is only a single, somewhat spherical organ in the centre of the fifth segment. In this work all descriptions of structure refer to the light-organs of the adult male. The main tracheæ of the photogenic segments send branches ventrad through the light-organs. Thus the dorsal surface in fresh

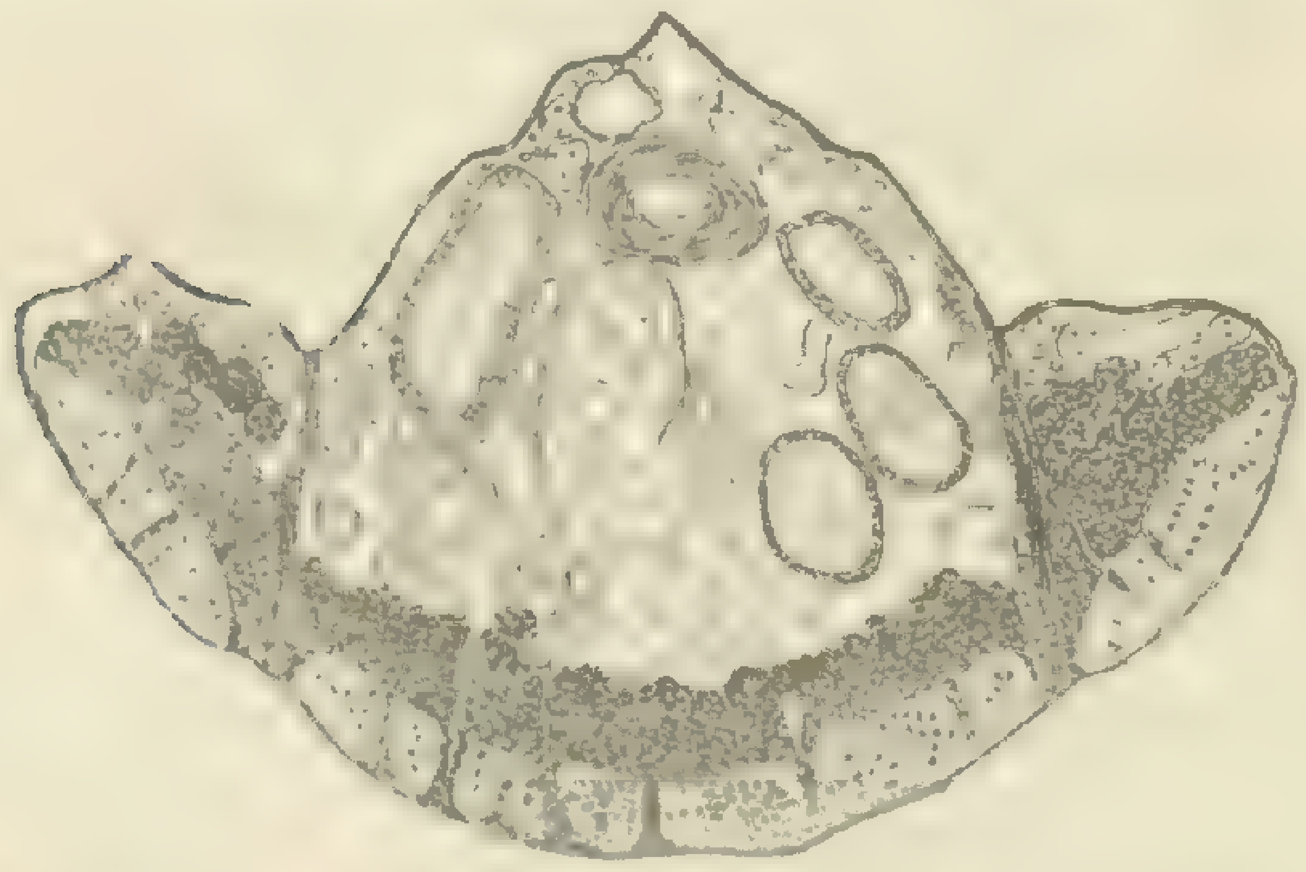


FIG. 1.— Transverse section through entire abdomen. × 20.

material is shown to be pentetrated by numerous tracheæ. The vertical or oblique tracheæ continue to branch profusely in an arborescent manner. This repeated branching is characteristic of the tracheæ of the photogenic tissues. The tracheal epithelium is composed of thin, flattened cells, with large flattened nuclei. Prominent hair-like projections of the intima are abundant in the lumen of the large tubes. These internal chitinous hairs have been noted in Lampyris by Gerstæcker, and in Luciola by Emery. The light-organs are innervated by nerves from the last two abdominal ganglia. These ganglia are both situated in the fifth segment, over the more cephalic light-plate. I failed to trace more than these primary nerve branches, as my attempts at methylene blue injection were unsuccessful.

Each light-plate is composed of two distinct layers, in this

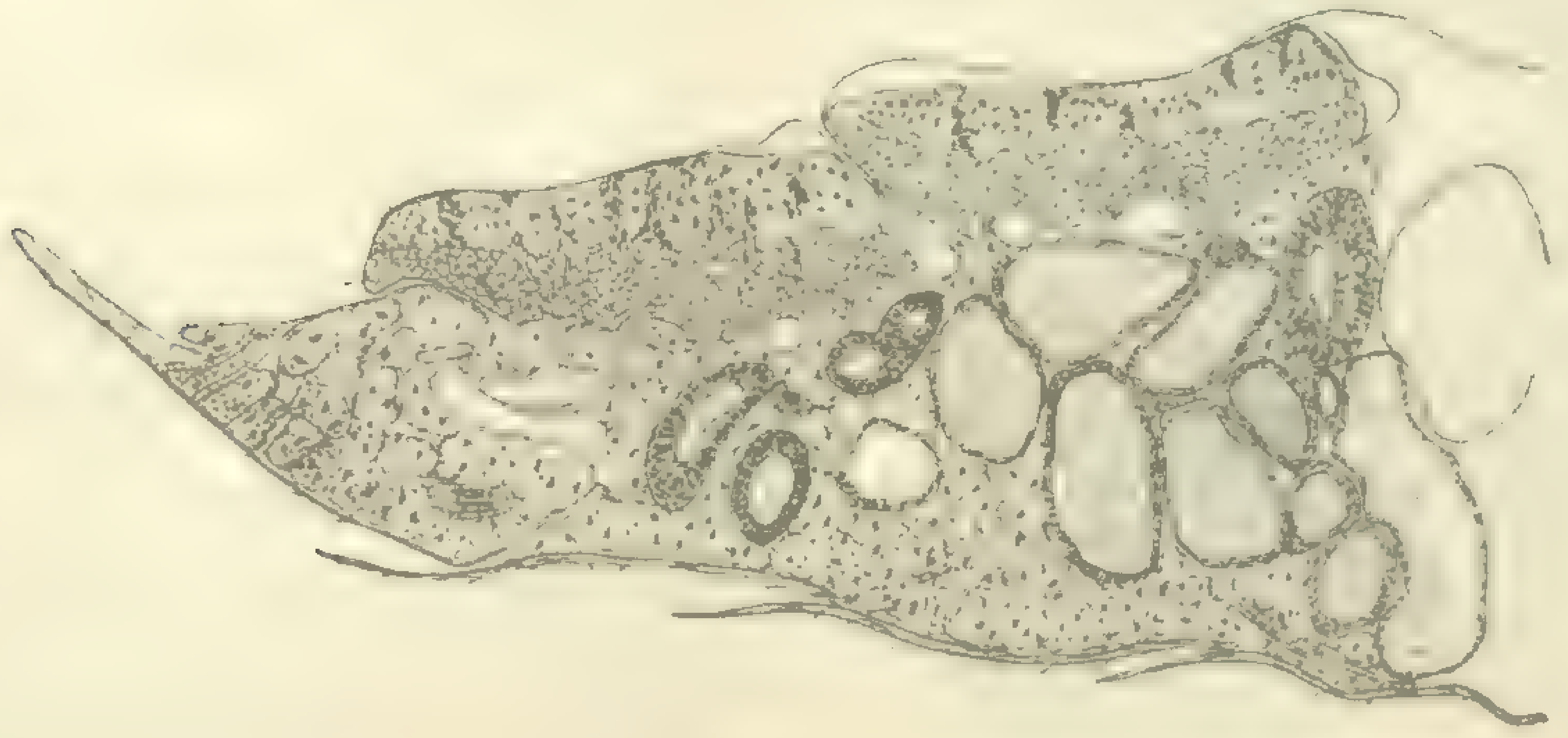


Fig. 2.—Longitudinal section through abdomen from fifth segment to caudal end. × 20.

respect agreeing in structure with the European species which have been studied. In none of my preparations have I been able to detect any trace of a membrane, either surrounding the light-organs or separating the two layers. Wielowiejski ('82) states that in *Lampyris splendidula* each light-plate is surrounded by a delicate film of connective tissue, in which small rounded nuclei may be faintly seen in well stained material. He gives no figures of this, however. Emery ('84) says there is no indication of a membrane in Luciola. The two layers cannot be distinguished in fresh material, but a difference in the two surfaces of the light-organ is apparent. The dorsal surface is a bright chalky white, while the ventral surface appears yellowish and luminous. Examined with a low power of the micro-

scope the dorsal surface is seen to be divided into polygonal areas.

The appearance of the cells of the dorsal layer varies much with the treatment of the tissue. Material fixed in alcohol and brought in contact with water for but a short time in staining with hematoxylin shows the cells filled with a dense content of coarse granules. With reflected light these granules still show their characteristic chalky whiteness, while with transmitted light they are brown. Granules identical in appearance are also found in the fat cells of the same region of the body. Material fixed in any fluid requiring subsequent washing in water shows a considerable decrease in the granules of the dorsal layer. This verifies the statement of Wielowiejski that these granules are insoluble in alcohol, but soluble in water. Kölliker, in 1857, proved them to be crystals of urate salts, and his results have been accepted by Wielowiejski and Emery. When the crystals have been dissolved out the form of the cells is easily determined. They are polygonal, fairly regular in outline and similar in size. They average about 28 μ by 25 μ. Those upon the upper surface are somewhat more spherical than those beneath. Large nuclei are always present, but the cytoplasm seems to have been almost entirely replaced by the granular secretion. (Fig. 3.)

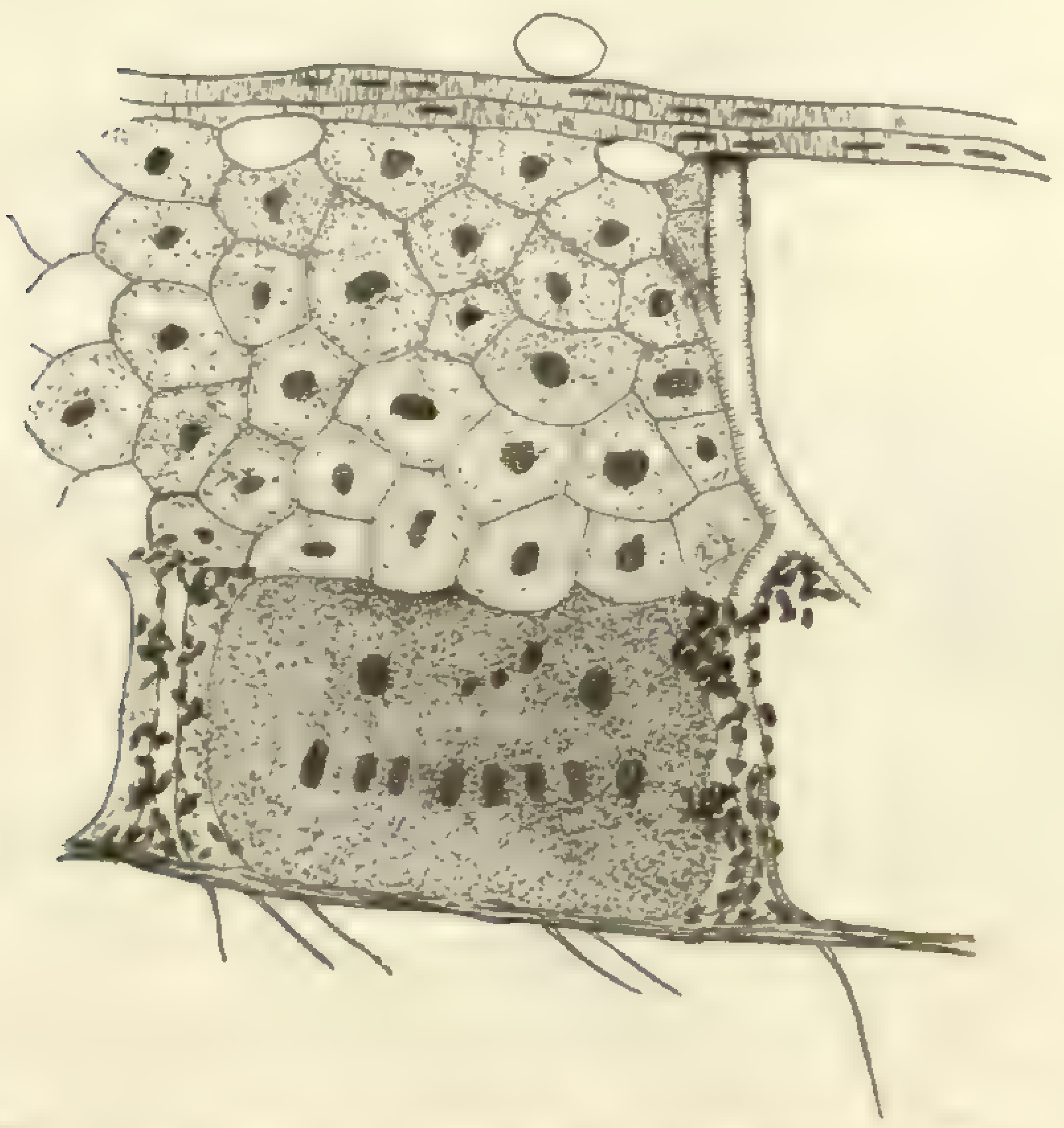


FIG. 3.—General features of both layers of light organ. Gilson's fluid, hematoxylin and eosin. × 75.

The dorsal layer not only forms a plate resting upon the ventral layer, but it projects beyond the latter and extends along its caudal surface to the body wall (Fig. 2). There are two groups of muscle fibres in each light plate, extending from the dorsal to the ventral body wall in the lateral portions of the plate. These muscles are surrounded by a layer of cells distinctly separated from the cells of the ventral layer and contin-

uous with those of the dorsal layer. In material in which the dark granules of the dorsal layer cells have not been dissolved out, they are found equally in the cells surrounding these groups of muscle. (Fig. 1.)

The ventral layer is composed of two distinct elements, the so-called parenchyma cells, and the cylinders. The cells of the parenchyma differ from those of the dorsal layer in being very irregular in shape and size. Occasional cells extend from the dorsal surface of the layer to the body wall. In some cases the depth is several times the thickness, while some cells are almost spherical. In some places the ventral layer is found to be several cells deep. (Fig. 4.) The size of the cells varies considerably. The granular secretion in these cells is much finer than that in the dorsal layer. Max Schultze has stated that these granules are of non-urate composition. He examined the granules of both layers with polarized light, finding that those from the dorsal layer were bi-refractive, but that those from the ventral layer were not. Those of the dorsal layer having been proved by Kolliker to be of urate composition, he concluded the granules of the ventral layer were non-urate. Wielowiejski verified the results of these experiments, but did not agree with Max Schultze's conclusions. He states that these experiments merely prove the granules of the ventral layer to be in general amorphous. He thought, however, that the difference in composition could be readily demonstrated by reagents. He found the granules of the dorsal layer to be soluble in water but insoluble in alcohol, while the opposite was true of those of the ventral layer. Emery says that the granules of the ventral layer are not crystalline, and that they disappear altogether in balsam preparations. The cells of the ventral layer appear to have more or less of granular content in all of my preparations, including those from material fixed in alcohol. It is only in osmic acid material that cells are found comparatively free from such secretion. As all my sections are mounted in balsam, this medium would not seem

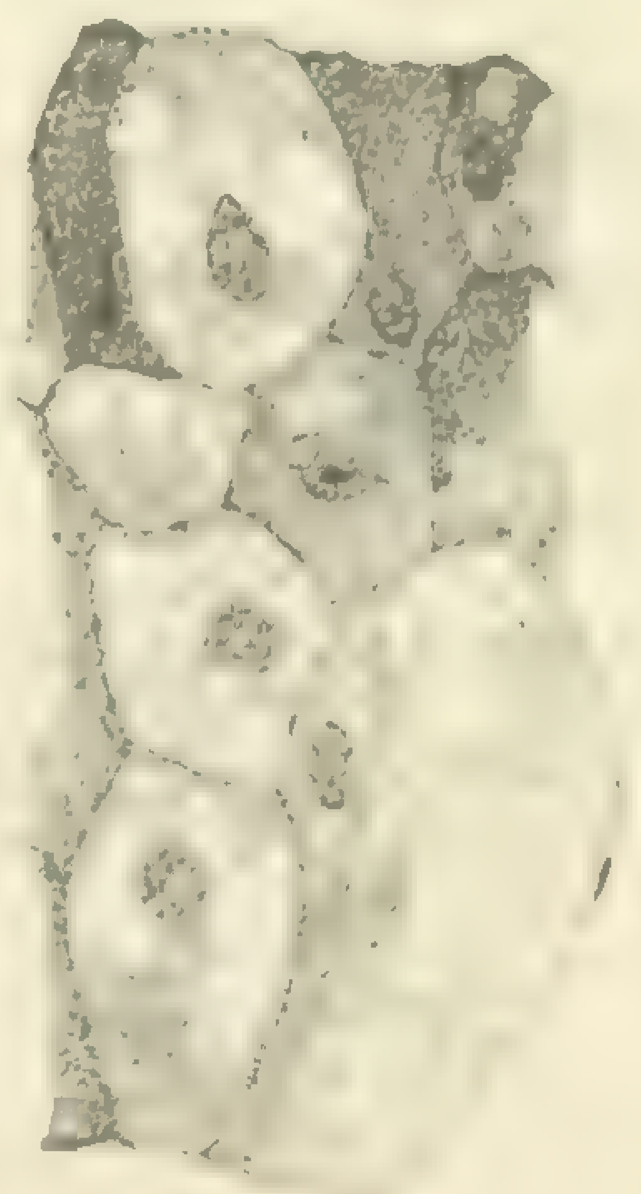


FIG. 4.—Cells of parenchyma. .3 % osmic acid. × 250.

to have any decided effect. This question, however, can be satisfactorily settled only by the study of fresh tissue.

Between the areas of parenchyma are sharply defined, more or less cylindrical masses of tissue surrounding the vertical tracheal stems and their branches. It is about these cylinders and their tracheæ that the greatest interest is centered. The cylinders are from 23 μ to 68 μ apart, and average about 30 μ in diameter. Their appearance differs greatly with the fixation. In material fixed in alcohol or Gilson's fluid, and stained with hematoxylin and eosin they appear as areas less granular, and consequently less deeply stained, than the intervening parenchyma. They contain a large number of small nuclei, especially abundant near the tracheæ. After fixation in Hermann's fluid and staining with safranin the cell outlines appear very distinct. (Figs. 10 and 11.) Preparations fixed in Flemming's solution and stained with safranin also show cellular structure, though not so definitely as the preceding. Less indication of the structure of the cylinders is shown in the osmic acid material.

If fresh material, placed for fifteen minutes in .5 % osmic acid and then treated for a few minutes with weak caustic potash, is viewed from the ventral surface, the cylinders appear as very distinct rings. In all preparations, both temporary and permanent, the boundaries of the cylinders are sharply defined.

Within each cylinder is a main tracheal stem which gives rise to numerous branches in the characteristic aborescent manner. There is no change in the structure of the tracheæ until near the periphery of the cylinder, where each fine tracheal twig breaks up into tracheoles. The number of tracheoles arising from one tracheal twig seems to vary somewhat. Ordinarily there appear to be only two, but three or four are not uncommon. Emery gives the number of tracheoles in Luciola as being uniformly two. In Lampyris, Wielowiejski found the number variable, as many as six sometimes occurring.

The tracheoles are fine tracheal branches and are characterized by having no spiral thickening of the intima. Their chitinous structure is plainly shown by the fact that they persist in material treated for some time with caustic potash.

Max Schultze, Targioni-Tozzetti ('70) and Emery were all of

the opinion that the tracheoles do not contain air, but a colorless fluid. Wielowiejski also found them filled with a fluid, but recognizing the extreme improbability of such condition existing in life, he looked for some explanation of it. In dried, air-filled material mounted in weak glycerine the tracheoles as well as the larger tracheal tubes were filled with air. After about five minutes the silvery, glistening lines of air became broken up,

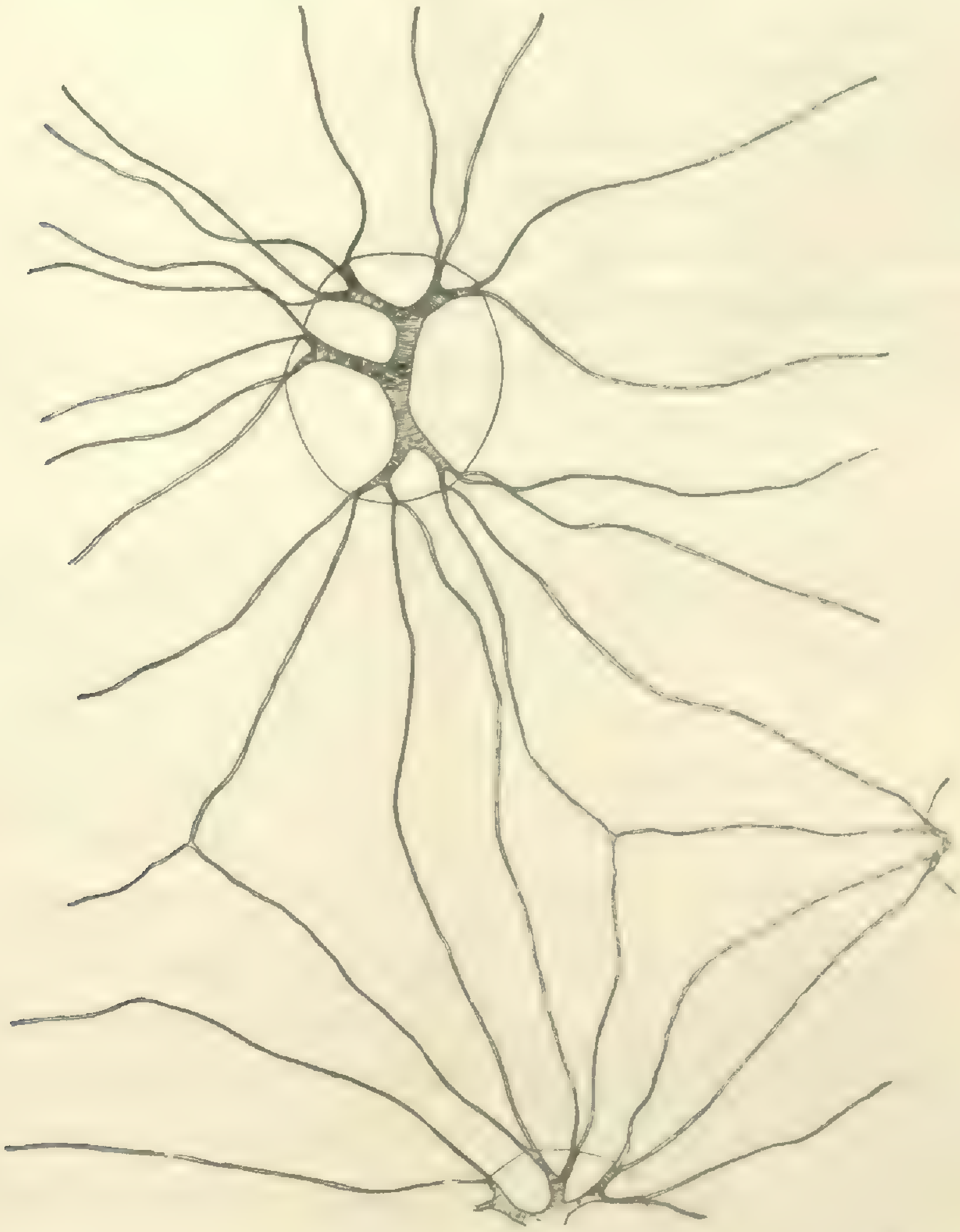


FIG. 5.—Teazed preparation, showing anastomosing of tracheoles.

and gradually, from the tracheoles in, the tracheæ became filled with a fluid. This would seem to prove, what one must believe *a priori*, that the entire tracheal system is filled with air. My observations agree with Wielowiejski's, for although in my preparations the tracheoles were always already filled with liquid, the penetration of the liquid into the larger branches was unmistakably from the tracheoles in. It may be noted in this con-

nection that in the tracheoles of developing wings, structures entirely similar to those of the light-organs, the presence of air may be readily seen.

In sections parallel to the axis of the cylinder the tracheoles are generally cut, so that their entire length cannot be followed. The fact that they appear to end free cannot, therefore, be taken as any proof. In rare cases they are seen to anastomose with those of adjacent cylinders, and in sections transverse to the cylinders, beautiful demonstrations of anastomosing may be seen. If a light-organ from a freshly killed insect is placed for a half hour in .5 osmic acid, then for a few minutes in caustic potash, and then placed under the microscope, ventral side up, the tracheoles can be easily seen. The cylinders stand out as definite circular or oval rings, and from the inclosed tracheæ radiate the tracheoles. As the distribution of the cylinders is fairly regular, the network of tracheoles has a notably uniform pattern. Tracheoles from three cylinders unite at a point about equidistant from their respective cylinders. (Fig. 5.) In preparations from material fixed in Flemming's, or Gilson's fluid, the same tracheolar network may be clearly seen. (Fig. 6.)

When the ventral surface of a fresh light-organ is studied under the microscope in a dark room the light is found universally distributed throughout the parenchymatous area. The cylinders stand out as non-photogenic spots on the background of light. This shows that the photogeny occurs in that portion of the tissue where the tracheolar network is found, and where there is consequently the most abundant supply of oxygen.

FIG. 6.—Anastomosing of tracheoles. Fleming's fluid, safranin. × 150.

Wielowiejski found anastomosing of the tracheoles generally true in Lampyris, although he admits of some exceptions to the rule. Wistinghausen and Holmgren found anastomosing of the tracheoles in the silk-glands of the caterpillar. Emery states

that in Luciola the tracheoles in all cases end free. This is shown in his figures 4 and 7, Plate XIX.

In Lampyris Wielowiejski figures the tracheoles as winding irregularly and twisted and looped about each other. In Photinus they are generally almost straight. They may be slightly wound about each other, but for the most part they pass directly from one cylinder to another.

Both Wielowiejski and Emery agree in considering that the tracheoles pass between the cells of the parenchyma, although positive proof is difficult. In no case has any portion of a tracheole been found within the parenchyma cells, although they have been seen closely applied to the exterior of the cells. In surface sections of Photinus the areas between the tracheoles would appear to correspond to cells, each possessing a nucleus. It thus seems altogether probable that in their course outside the cylinders the tracheoles are intercellular.

In 1864 Max Schultze studied the light organs of *Lampyris splendidula*, using osmic acid as a fixer. He found the finer tracheal branches losing their spiral thickening and passing into star-shaped, finely granular bodies which he believed to be true cells possessing distinct nuclei and cell membranes. He failed to find any continuation of the tracheæ beyond these stellate cells, and so assumed that these cells enclosed the ultimate endings of the tracheæ. The name "tracheal end-cells," as given by Max Schultze has since been generally used, even by those who knew it to be a misnomer.

In his studies of the same species, Wielowiejski found the tracheæ passing into the stellate "end-cells" of Max Schultze, but instead of ending there, branching to form tracheoles which penetrate the inter-cylindrical parenchyma. He believed these "end-cells" to be true cells, much flattened and similar in form to the endothelial cells of vertebrates. They extend about the bases of the tracheoles in a web-like manner and are more or less stellate in shape. These cells show a characteristic reaction with osmic acid, causing a precipitate to be formed, especially about the point of origin of the tracheoles. The tracheal twig appears constricted at its apex, and is intensely blackened by the osmic acid. The effect of the acid varies, in some cases the entire end cell being uniformly blackened.

In the female of *Lampyris noctiluca* and the female and larva of *Lampyris splendidula* Wielowiejski found a somewhat different condition than in the adult male of *L. splendidula*. The tracheoles arising from the ends of the finer tracheæ are generally only two in number. They may also occur along the course of the smaller tracheæ, instead of only at the ends, and they may even arise from some of the larger tracheal branches. It is obvious that under such conditions "end-cells" like those figured for *L. splendidula* would not be present. He states, however, that there is a membrane spread out between the tracheoles, although it fails to give the characteristic "end-cell" reduction with osmic acid. From the larva of *L. noctiluca* he figures one of the larger tracheæ with its branches, with a strongly developed, nucleated membrane surrounding it much as a cylinder surrounds the tracheal axis in the imago of Photinus. The epithelium of the large primary trunks of the tracheæ in the larva shows the power of precipitating osmic acid.

Wielowiejski also studied tracheal endings in other parts of the adult *L. splendidula*. In the fat body and reproductive organs he found "end-cells" in abundance, similar to the typical ones of the light-organs in their reaction with osmic acid, but differing considerably in shape and in the number of tracheoles contained. In all these instances Wielowiejski interprets the "end-cells" as being a special development of the epithelium of the trachea. In his figures the tracheæ, before entering the photogenic tissue, show well developed epithelium, this layer being sometimes almost as thick as the diameter of the tube.

Wielowiejski neither figures nor describes cylinders in the light-organs of Lampyris. After his study of *Luciola italica* ('86) he states that he found no such regular arrangement of the tracheæ here as occurs in the two species of Lampyris formerly studied. He did not consider the mass of the cylinders in Luciola as homologous with the "end-cells" of Lampyris.

In *Luciola italica* Emery found the ventral layer composed of cylinders and intermediate areas of parenchyma much as has been already described for Photinus. In osmic acid preparations he saw, just within the periphery of the cylinder, small, irregular, three-cornered masses, in which the distal ends of the tracheæ

and bases of the tracheoles appeared to be imbedded. When a tracheal axis was isolated these small bodies looked like "grapes on a stem," while from each "grape" two tracheoles proceeded. As these browned bodies were found only in the osmic acid preparations he believed them to be artifacts, and not the "tracheal end-cells" of Max Schultze. He concluded that the clear cell elements of the cylinder are the real "end-cells." Within these the tracheæ undergo their final division, each giving rise to two tracheoles. In Luciola only that part of the cell which is in direct contact with the bases of the tracheoles is blackened by osmic acid.

Emery agrees with Wielowiejski in considering that the "end-cells" are formed from the tracheal epithelium.

Two of the latest investigators of tracheal endings, Wistinghausen and Holmgren, have both worked on the silk-glands of lepidopterous larvæ. Both found the finer tracheæ passing over into what they term the "tracheal capillary end-network," a network formed by the anastomosing of the tracheoles and their branches. They agree in stating that the epithelium of the tracheoles is extended in a web-like manner to form the "end-cells." Holmgren discards the term "end-cells," substituting for it the more correct name of "transition cells," as these structures form the transition between the tracheal tubes proper and the tracheolar net-work.

In the light-organs of Photinus, fixed for thirty hours in .1 % osmic acid and stained with safranin, the transition cells may be seen most plainly. They show with varying

FIG. 7.—Transition cells in typical osmic acid preparation. × 250.

clearness in all the osmic acid material, and in one insect fixed in Flemming's fluid. In the typical osmic acid preparation they appear as irregularly spherical bodies, blackened throughout but most intensely so at the point of origin of the tracheoles. They show no appearance of nuclei, but as the nuclei of the adjacent cells show only faintly with this treatment, this is not significant.

The transition cells of Photinus as shown in osmic acid preparations are more similar to the blackened, grape-like bodies described by Emery, than to the stellate, endothelioid cells figured by Wielowiejski. They occur at the apices of the finer

FIG. 8.— Transition cells where effect of osmic acid has been less pronounced. × 300.

tracheal twigs, and near the periphery of the cylinder. The space between them and the tracheal axis, and the spaces between the transition cells themselves appear clear. The edges of the spheroid masses are generally irregular, and their whole appearance suggests an artificial condition. (Fig. 7.) In sections where the effect of the osmic acid has not been as extensive, the same blackening at the points of tracheolar origin may be seen, but instead of finding spherical bodies surrounding these points of furcation, the granular mass of the cylinder appears in different condition. It extends along the periphery of the

cylinder, and follows the course of each tracheal branch, in some cases almost to the main stem, so that instead of a structure resembling a cluster of grapes, one finds along the wall of the cylinder a series of fan-shaped masses, one for each tracheal twig, their apices toward the axis of the cylinder. (Fig. 8.) As there is great irregularity in the form of these dark bodies within the cylinder, and also in the shape of the intervening clear spaces, it would seem that Emery is correct in considering them an artifact.

Definite cellular structure can be seen only in the material fixed in Hermann's and Flemming's fluids. In these preparations, as in those from osmic acid, the tissue seems to be shrunken and distorted. To a large extent the nuclei appear to have been separated from the cytoplasm, and to lie in the spaces left by the shrinkage of the cells. The cells show a tendency to shrink away from each other, and away from the main axis of the trachea, thus becoming smaller, denser bodies surrounding the distal ends of the tracheal branches, and in contact with the periphery of the cylinder. (Figs. 9 & 10.)

In material fixed in alcohol or Gilson's fluid there is no appearance of cells within the cylinder, although an abundance of small nuclei may be clearly seen.

Emery suggests that the cylinder, in Luciola, may be a syncytium, but in both longitudinal and transverse sections of the cylinders in material of Photinus fixed in Hermann's fluid, the cells are clearly demonstrated.

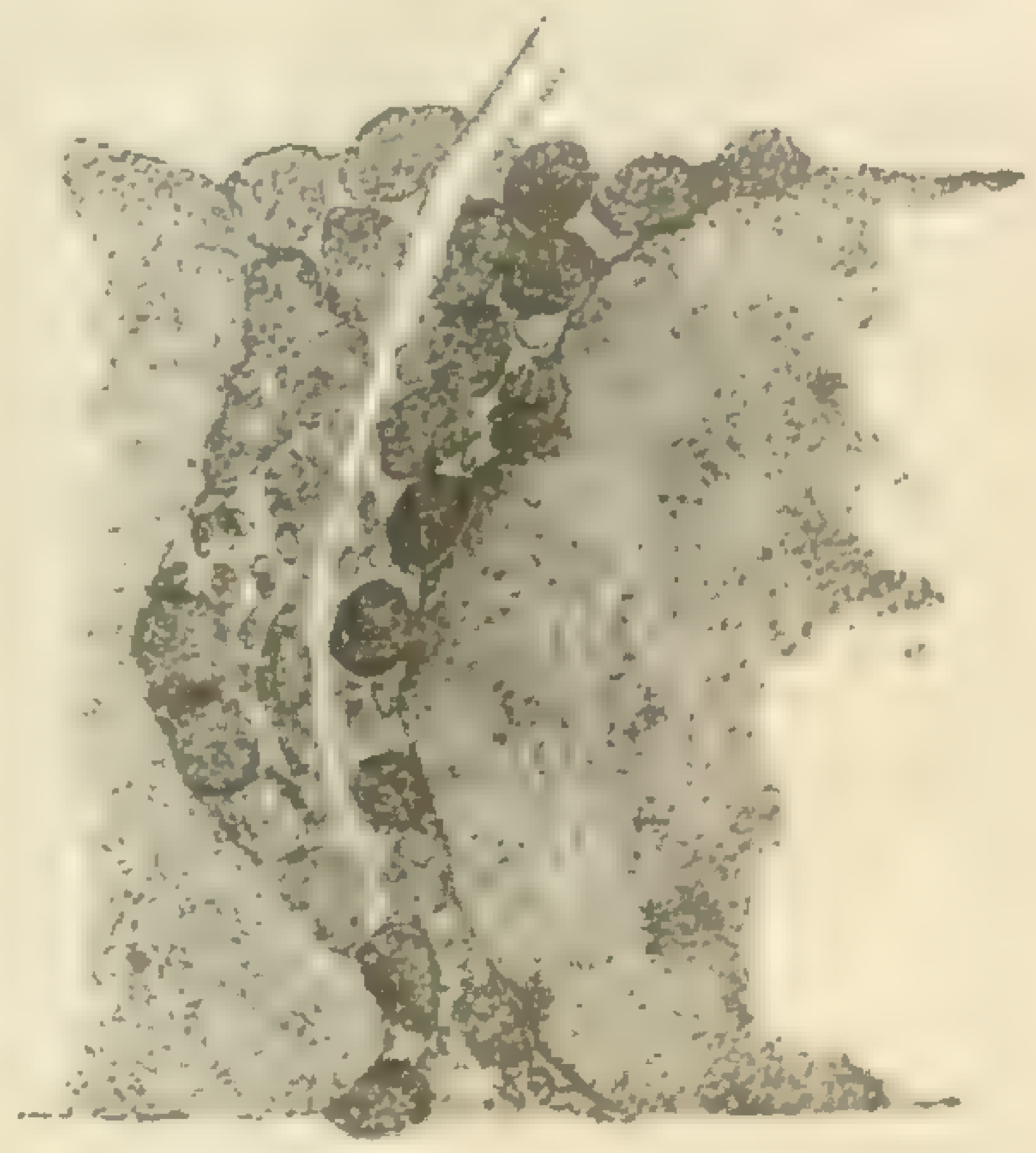


Fig. 9.— Section parallel to axis of cylinder. Herman's fluid. × 235.

The "end-cells" of Lampyris and the cylinders of Luciola are stated to be a special development of the tracheal epithelium. This is not true of the cylinders in Photinus, as the epithelium can be definitely seen, not only in the tracheal axis, but even in the small branches. (Fig. 11.) The epithelium of the tracheæ of the photogenic tissue is altogether different from that figured by Wielowiejski for Lampyris. Instead

of being thick, it is very thin, with large flattened nuclei. In both longitudinal and transverse sections, where a nuclear stain has been used, the epithelium may be readily traced within the cylinders, even to the finer branches. It is exactly similar in appearance to that in the dorsal layer, and is wholly distinct from the cellular elements of the cylinder. Small flat nuclei are seen closely applied to the tracheæ, while the irregular nuclei of the cylinder cells lie at a little distance away.

In his study of Luciola in 1886, Wielowiejski did not find the cylinder a syncytium, as stated by Emery, but believed it to be composed of two elements, a nucleated epithelium immediately surrounding the trachea, and an outer layer belonging to the parenchyma. The latter he found generally separated from the trachea by the action of reagents, but still connected with the parenchyma cells. These observations would seem to be in agreement with the conditions found in Photinus.

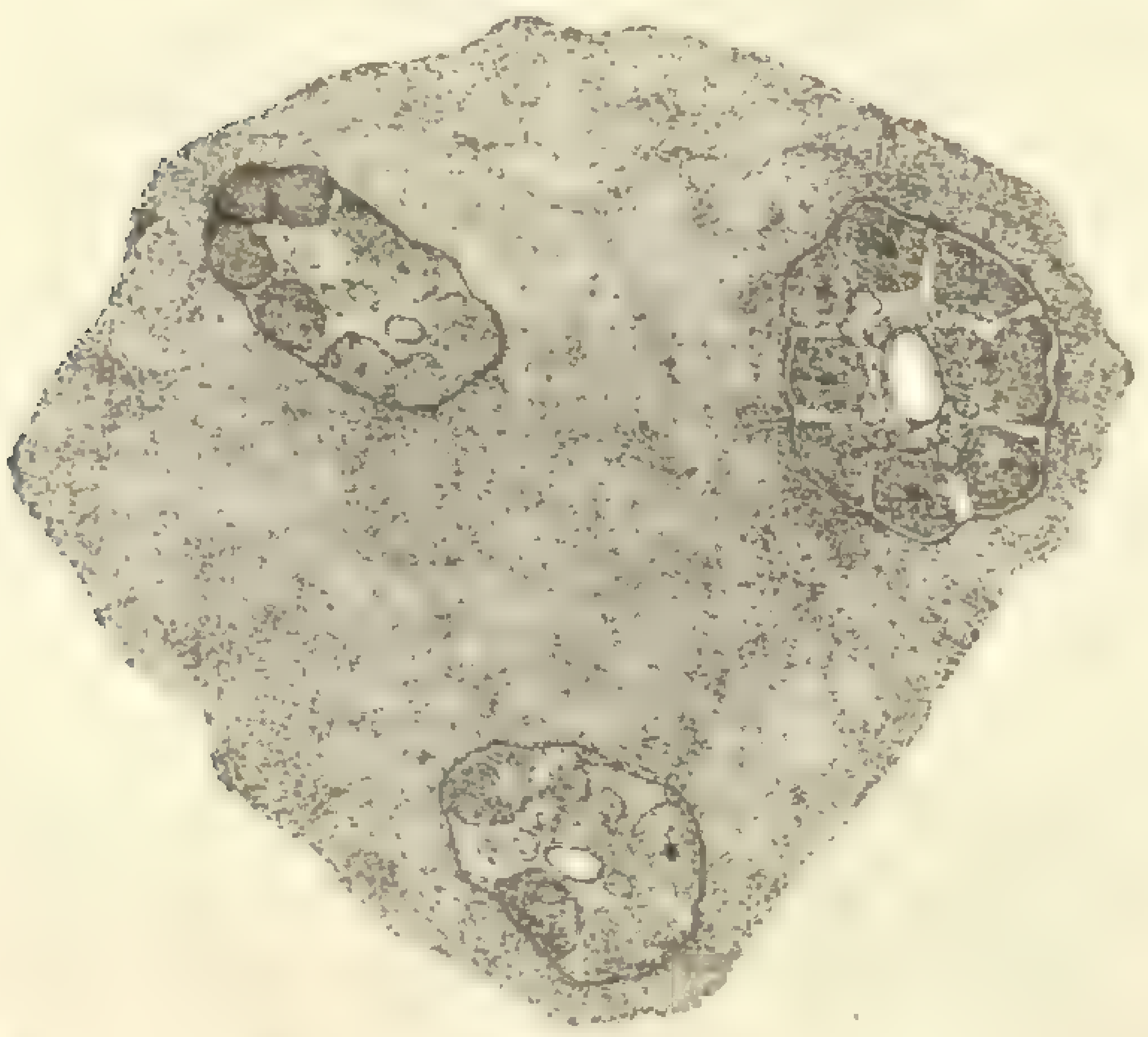


FIG. 10.—Section transverse to cylinder. Herman's fluid. × 235.

The bulk of the cylinder is thus shown not to be of tracheal origin. The tracheæ pass into the cylinder cells, there dividing to form the tracheoles, so that the name "transition cells" is equally befitting here, although the structures to which it is applied cannot be considered homologous with those of the "capillary end-network" of the caterpillar. If the cylinders belong to the parenchyma, they are at least clearly distinguished from it by definite boundary lines. In some cases there might seem to be a transition between the cells of the dorsal layer and those of the cylinder, but the cylinder cells are much smaller than those of either the dorsal layer or the parenchyma. They retain their spherical shape much more than either of the others mentioned. It would seem probable that all

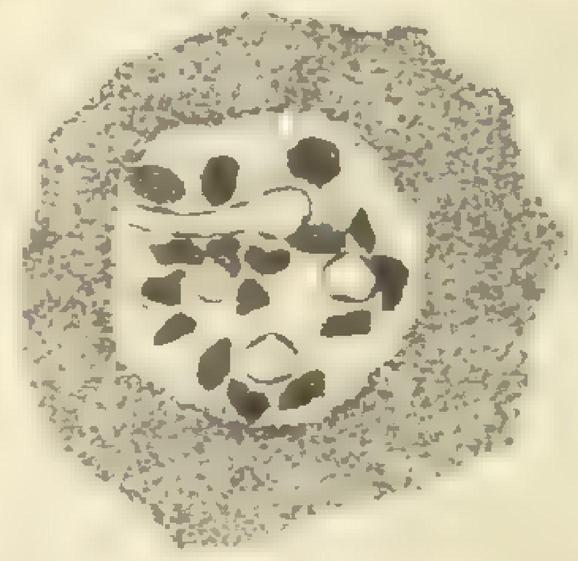


FIG. 11.—Section through cylinder showing epithelium of trachea. × 235.

three forms of cells are of the same origin and that their structural differences are due to difference in function.

Wielowiejski, from his work on *Lampyris splendidula* believed in the possible transformation of the parenchyma cells of the ventral layer into the cells of the dorsal layer through the physiological effects of photogeny. Emery did not accept this theory, and after his study of Luciola and two American species of Lampyridæ, Wielowiejski himself ('89) stated that, for those forms at least, it was untenable.

The conditions in Photinus are such as to apparently preclude such an hypothesis. The two layers are distinctly separate in all preparations and the relative thickness of the layers is fairly constant. There is no indication of a transition between the two layers, nor is there any apparent difference in the thickness of the layers in material put up in early summer and in that taken at the close of the flying season. Still more important are the inherent differences in the two layers. In the dorsal layer there is a solid mass of polygonal cells, similar in form and size, and irregularly penetrated by tracheæ. In the ventral layer there is a distinct division into two elements, the cylinders enclosing the tracheal trees, and the parenchyma cells. The arrangement and distribution of the tracheæ of the ventral layer is strikingly regular. The parenchyma cells are extremely irregular, both in form and size. It would, therefore, seem difficult to suppose that the dorsal layer could grow at the expense of the ventral layer.

Several theories have been offered as to the origin of the photogenic tissue. Kölliker ('57) regarded the light organs as "nervous apparatus." Owsjannikow ('68) thought them of epithelial origin. Wielowiejski ('86) suggests their derivation from the "kleine Œnocyten" which he finds absent in the photogenic species of Coleoptera. The most general view, however, is that the photogenic tissue is differentiated fat body. This is upheld by a general similarity in structure, position and cell content. It has been already noted that granules exactly similar in appearance to the urate crystals of the dorsal layer have been found in the fat body near the light organs.

A question of this character could be settled only by onto-

genetic study of the photogenic tissue. This has not been attempted, so far as I can learn, by anyone besides Dubois ('98). He has studied the development of both *Lampyris noctiluca* and *Pyrophorus noctilucus* from the earliest stages. The eggs were found to be luminous even before they were laid, so that the light was transmitted in unbroken continuity from one generation to the next. Dubois followed the development of the light organs through all the different changes occurring from the beginning of segmentation to the emerging of the adult insect, and his observations led him to state definitely that the photogenic tissue is derived directly from the underlying hypodermis, by a proliferation of these cells. He also states that in the development of the organs a transformation takes place in the protoplasm of the cells, the older cells toward the upper surface of the light organs becoming filled with opaque, chalky granules. The younger cells, in which this transformation has not taken place, constitute the parenchyma.

While these results are not in line with previously accepted ideas in regard to the derivation of the light organs, they are based upon the only kind of study which can determine the problem. Apparently Dubois's work has not been generally accepted, and it needs verification by other workers. Nothing could be more profitable in our present state of knowledge than extensive and thorough study of the photogenic tissue throughout all its transformations.

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ORAL BREATHING VALVES OF TELEOSTS, THEIR MODIFICATIONS AND RELATION TO THE SHAPE OF THE MOUTH.

EVELYN GROESBEECK MITCHELL.

ALTHOUGH the oral breathing valves of teleost fishes are very prominent and their function important, they have, strangely enough, been almost wholly neglected. Owen ('66), suggests that they "seem intended to prevent the reflux of the respiratory stream." Macullum ('84) mentions them in his article on Amiurus but ascribes to them no function. Stannius ('39) has described them, as has also Cuvier ('36) who suggests that they not only prevent the reflux of water but the escape of food. Galton ('71), describes the valves and their working in detail, much as Dahlgren ('98) did later. Howes ('83), refers to them in the trout, explaining their function.

In 1898 Dahlgren, who knew nothing of Galton's article,[1] took up the subject in detail and describes the valves in the sunfish, *Eupomotus gibbosus*. The valves are sheets of membrane composed of elastic connective tissue covered with a mucous membrane continuous with that lining the mouth. They are situated in the oral cavity just caudad of the maxillary and mandibular teeth. In this species of sunfish there is a median muscular thickening. The valves "are placed with their edges pointing downward and backward at an angle of less than forty-five degrees to the axis of the body. This angle is increased to about eighty degrees when the valves are struck by the regurgitating stream of water."

The function of the oral valves is to aid in the act of breathing, which has hitherto been described as "a kind of swallowing."

Dahlgren says, "The respiratory stream enters the oral cavity by the mouth and leaves by the two gill openings." . . . .

[1] His attention has since been called to it by the present writer.

"In inspiration the stream enters at the mouth in response to a dilation of the oral cavity produced by the outward lateral movement of the opercular frames.

"At the same time water is prevented from entering at the gill openings by the brancheostegal valves which although they are attached to the opercular frames, move independently of and contrary to them; so that, while this outward movement of the frames extends the gill openings, the brancheostegal valves close them automatically by the action of the water which tries to enter.

"In inspiration the water is forced out of the gill openings by a corresponding contraction of the oral cavity. At the same time the water is prevented from regurgitating through the mouth, not by the contraction of the latter, but by the automatic operation of the maxillary and mandibular breathing valves which move as accurately and efficiently as any of the heart's valves. Caught on their posterior edges by the first movement of regurgitation, they snap together and completely prevent the water from leaving the oral cavity by the mouth which, meanwhile, is left partly open, almost as much open as during inspiration.

"That these valves are of value as breathing organs is evident upon casual observation; that they are of much importance is shown by the compensatory action, brought about by injury; that they are not of immediate vital importance is proved by the fishes' ability to get along without their services until they are repaired."

In examining about 70 species of fishes, the writer finds two types of valves. These she has called the crescentic and the U-shaped types. (Fig. 1.) There is a third form which may, however, be considered as a modification of either type and will be described later.

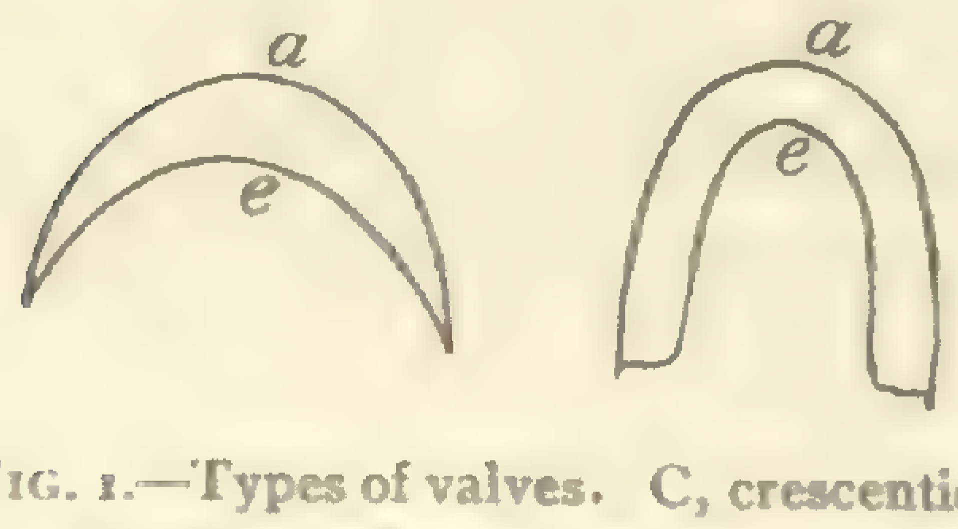

FIG. 1.—Types of valves. C, crescentic; U, u-shaped type. *a*, attachment; e, free edge.

The crescentic type of valve is typically shown in the catfishes, Siluridæ, particularly in *Schilbeodes punctatus*. This type of valve, as its name indicates, is in the form of a crescent with tapering ends, and may be broad or narrow. That of *Eupomotus gibbosus* is also of this type. The

free edge of the crescent is not necessarily a perfect curve (Fig. 2, *a*), but may be interrupted by a projection or a notch. (Fig. 2, *b*, *c*, *d*.)

In the U-shaped type, the ends do not taper but are bluntly truncate. (Fig. 1, *u*.) The free margin in these also may be perfect or interrupted.

FIG. 2.— Forms of free margin. *a*, perfect; *b*, projection; *c*, notched; *d*, fastened each side of meson; *e*, squared

A number of interesting modifications occur. As before mentioned, the free edges are often interrupted and in some cases, as in *Pomolobus pseudoharengus* and *Pomolobus æstivalis*, are attached near or at the meson, in one or two lines, to the roof of the oral cavity. (Fig. 3.)

The central thickening which Dahlgren mentions may be a tooth-like projection, may extend only halfway to the free margin or back between the tooth pads, may be straight, wedge-shaped, semi-circular (in this case the flat side was against the attachment), or may be round, this form being either at the meson on the attachment or in the center of the valve. (Fig. 4.) In one case, that of *Ameiurus natalis*, a horizontal thickening passed through the round centrally situated, mesal thickening. (Fig. 4, *j*.) The thickenings may be found in either or both valves. They appear to be muscular. Their function may be to strengthen, possibly to tighten, the valves, as they are found on the larger valve when the valves are of unequal size, and this valve

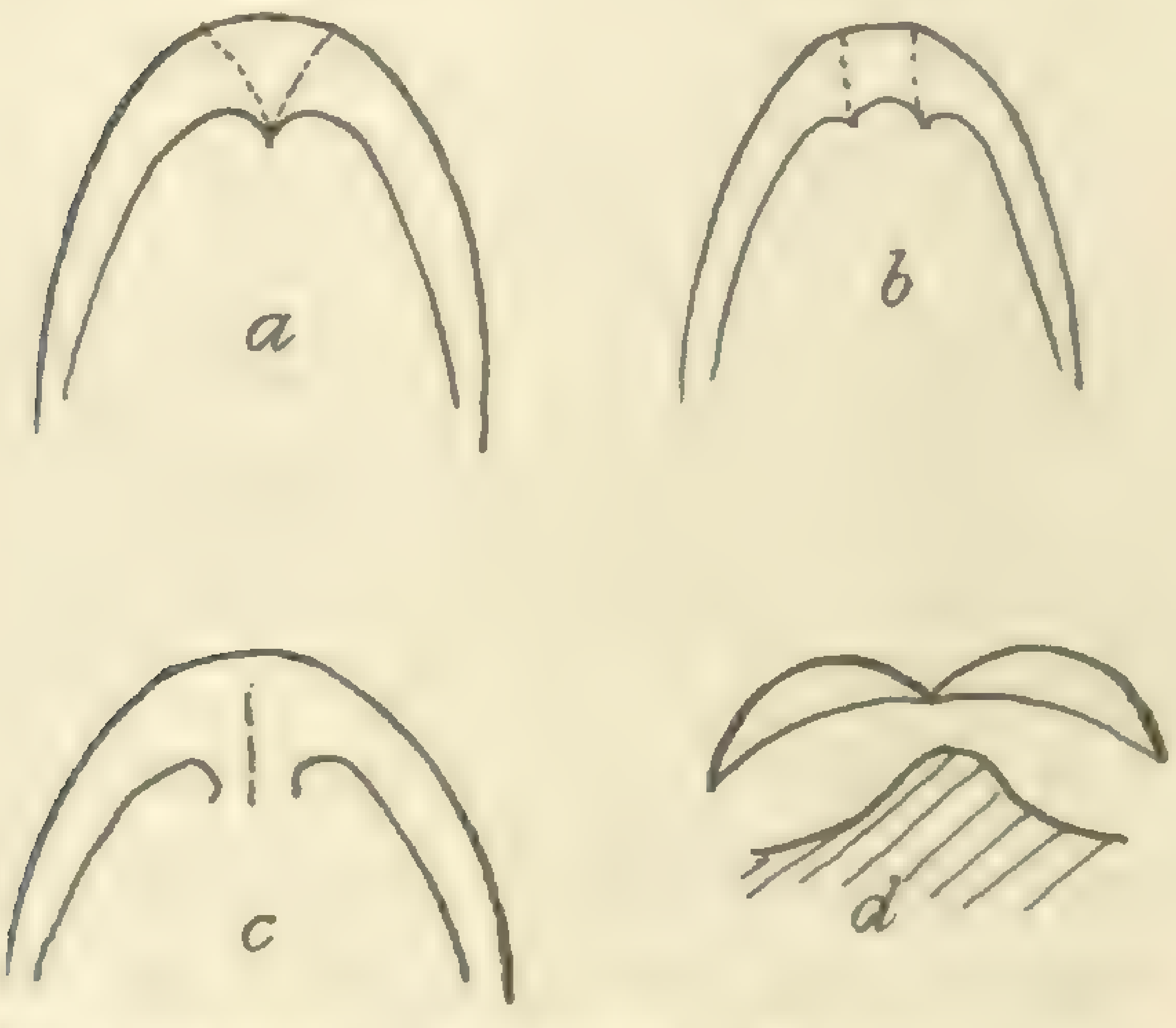

FIG. 3.—Attachment of free edges of maxillary valve at or near meson. *a*, *Clupea pseudoharengus* (v-shaped attachment; *b*, *æstivalis* (parallel attachment; *c*, Dorosoma (median linear attachment); *d*, Astrocopus (median point attachment).

is the more subject to strain and injury from its size and position. What is meant by "position" will be explained in the

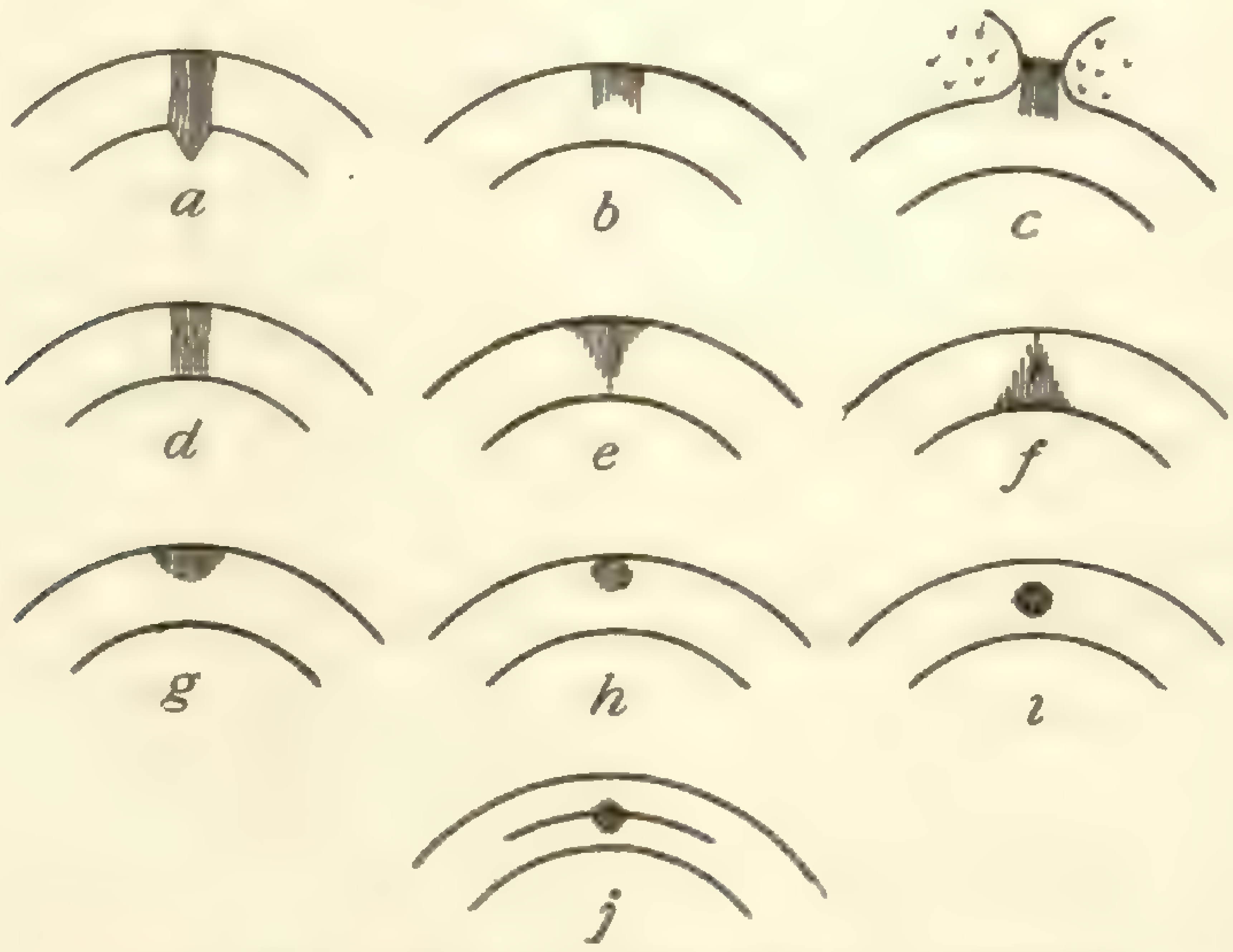

Fig. 4.— Forms of central thickenings. *b*, tooth-pads.

paragraph on the relationship of the valves to the shape of the mouth.

In the majority of species examined, papillæ are found on the valves. These papillæ vary widely in size and arrangement. They may be in almost regular rows, scattered, cover the whole valve or only a part of it, even, as in *Cynoscion nebulosus*, run back among the teeth. They may be coarsely setiform, flattened, rounded, on a stalk or, in one case, of a circumvallate appearance. (Figs. 5 and 6.) In some cases the papillæ are fine and closely arranged in rows, giving the appearance of short vertical rows or folds. (Fig. 5*c*.) These are easily distinguished from the true folds found on some valves. These papillæ at first appeared to be one elongated papillus but proved to be as described. In *Ambloplytes gruniens* are found rugæ surmounted by small papillæ.

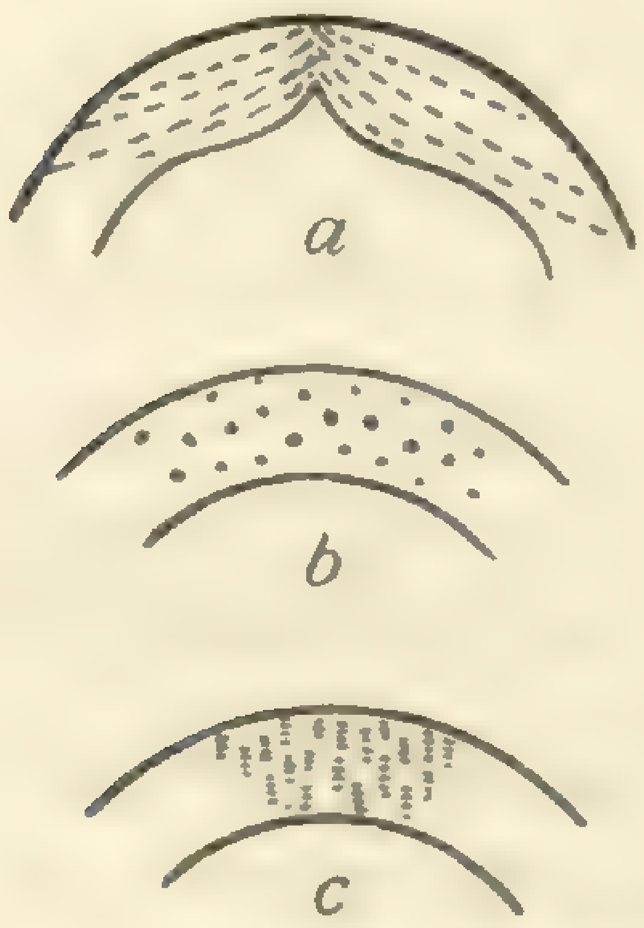

Fig. 5. — Some typical arrangements of papillæ. *a*, in lines; *b*, irregularly scattered; *c*, in short rows so that they resemble a number of small thickenings or folds.

A third kind of valve has been mentioned as being a modification of either the crescentic or U-type. The writer was for a long time greatly perplexed because many of the Cyprinidæ

apparently had no mandibular valve, yet, from the shape of the mouth, there was every reason to expect a small one. Finally in a large specimen of *Semotilus atromaculatus* it was seen that the place of the valve was taken by several rows of tall papillæ. (Fig. 6, *d.*) This was found to be the condition in all the minnows where the mandibular valve seemed absent.

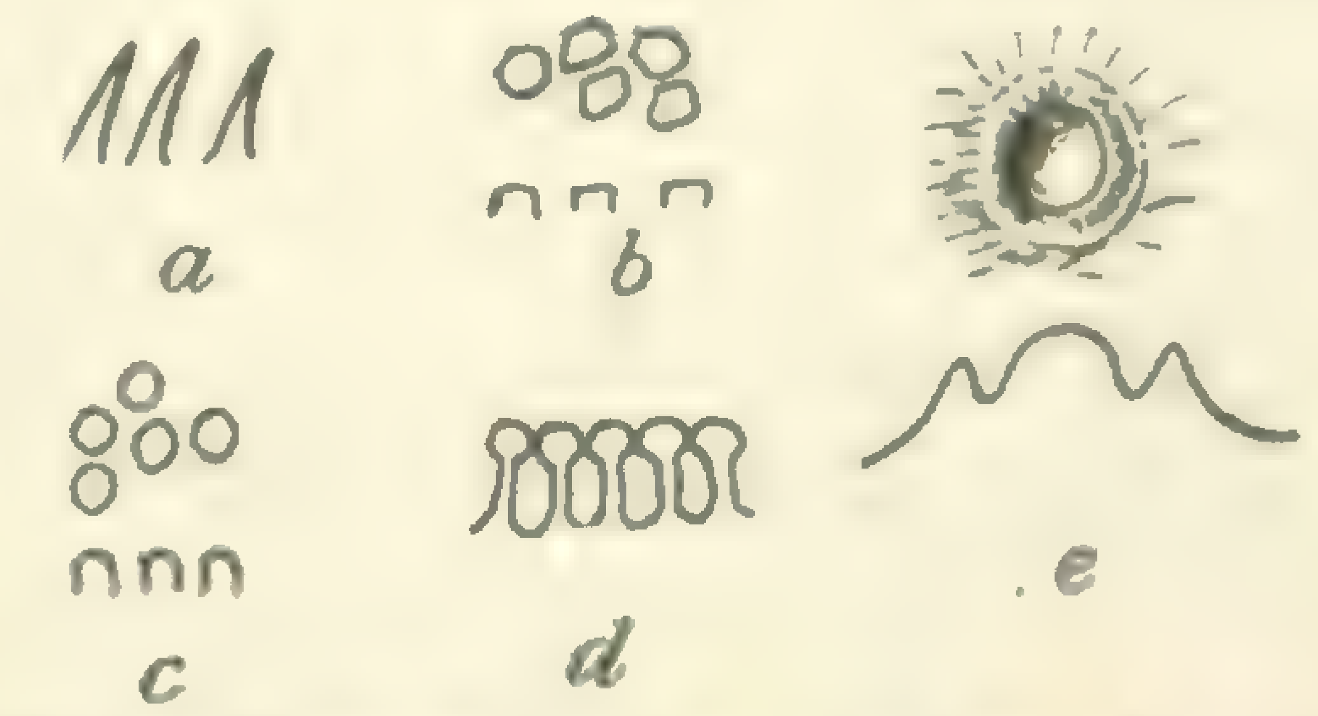

FIG. 6.—Forms of papillæ. *a*, setiform; *b*, vertical section and surface view of the flattened papillæ; *c*, wounded; *d*, stalked. *e*, circumvallate.

The function of the papillæ may be to aid in the finding of food. The best development of papillæ seems to be among the bottom feeders, where such sense organs would be most useful. Another modification of the valves is in the pigment which is frequently found in one or both valves. The pigment spots may be regularly arranged or scattered like the papillæ the arrangement varying with the species.

Some valves are further distinguished by rugæ or folds or by

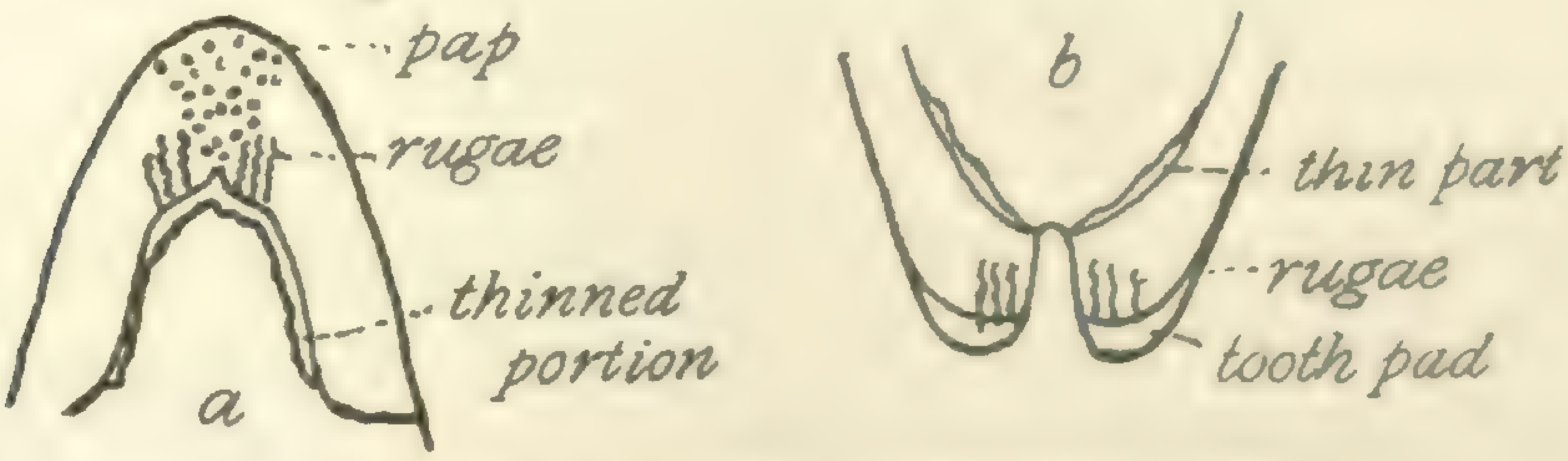

FIG. 7.—Valves of *A. gruniens*. *a*, maxillary; *C*, mandibular.

very thin and transparent margins or both as in the case of *Ambloplytes gruniens* (Fig. 7).

As before stated, the valves are not ever of quite equal size. Their size and shape are dependent on the size and shape of the mouth. For instance, in the case of the Siluridæ, (Fig. 8, *a*) the mouth is terminal, practically horizontal and very wide. For this reason it does not need to be opened far to admit the requisite amount of water, therefore the valves are long and crescentic but only of moderate depth, (*i. e.* the distance from attachment to margin). The mouth being horizontal, the regurgitated stream strikes the two valves with about equal force; therefore, both must be well developed.

In the Catostomidæ, or suckers, the case is very different. Here the mouth is inferior, (Fig. 7, *c*), and the snout depressed. In this family the maxillary valve is well developed and very deep. There are two reasons for this. First, the mouth of the sucker is not wide and must be opened farther; second, the lower valve is entirely absent. The reason for this is obvious. The depressed snout decurves the regurgitated stream, which strikes the upper valve only, hence a lower valve is not necessary, the edge of the upper valve catching against the lower jaw.

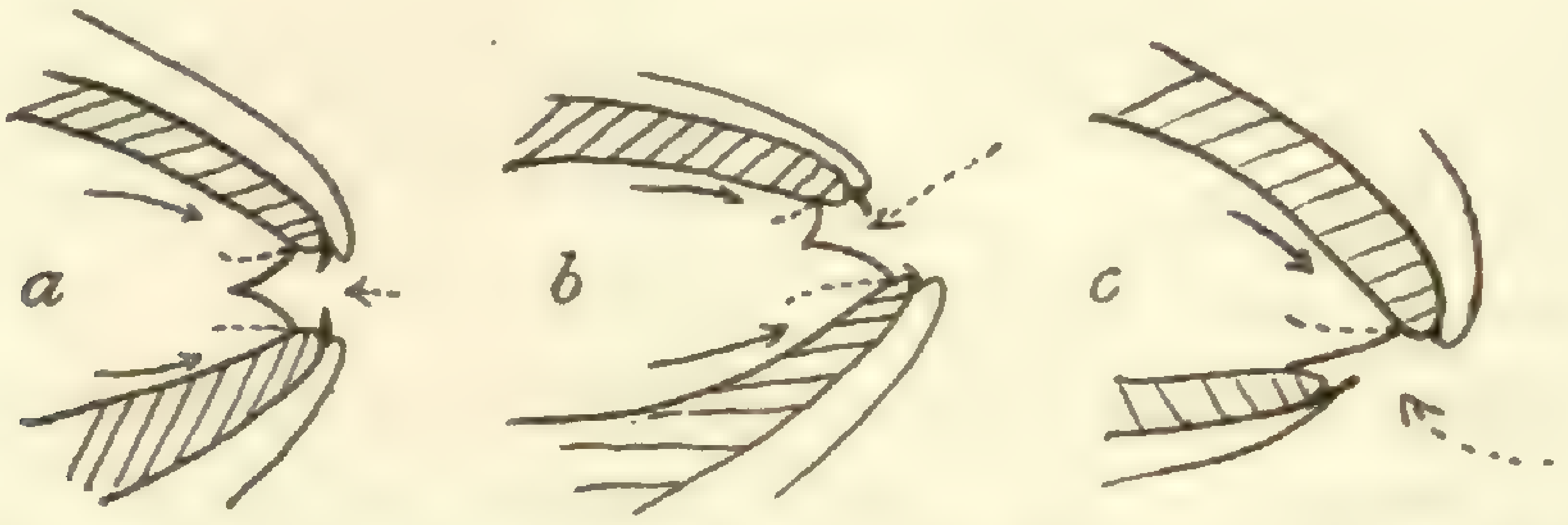

FIG. 8.—*a*, sagittal section showing incurrent and excurrent streams and position of valves when open and closed in horizontal mouth. *b*, similar section in superior mouth; *c*, in inferior mouth.

The position of the maxillary valve in these fishes is nearly horizontal, this being a better position to catch the returning stream. In the case of the minnows whose mandibular valve is replaced by papillæ, and in the case of some other fishes with maxillary valves much larger than the mandibular valves, the mouth is apparently horizontal or even slightly oblique. In all such cases, however, either the snout is depressed or the premaxillary is protractile and is held protracted when the fish is breathing quietly, thus depressing the snout and deflecting the greater part of the water against the maxillary valve.

As may be inferred from the foregoing, the fishes with true oblique mouths possess large mandibular and small maxillary valves. The latter are never completely absent but may be very small. The case of *Astroscopus y-græcum*, the "stargazer," might be supposed to form an exception to this rule, as the mouth is really superior. From analogy it might be supposed that the maxillary valve would be lacking. Such, however, is not the case. There is a well developed maxillary valve (Fig. 3), like two crescentic valves joined at the meson by their ends.

The reason for this structure is easily seen when the floor of the oral cavity is examined.

This floor is raised in the center and hollowed at each side in such manner as to divide the outgoing stream into two, and the corresponding part of the roof is so shaped and hollowed as to deflect the stream somewhat, so that notwithstanding the superior position of the mouth, the upper valve is necessary.

In *Echensis naucratis*, where the mouth is truly superior, there is a small maxillary valve, whose greatest width is on the parts each side of the meson about half way to the ends. This also can be accounted for by the hollowing out of the roof of the oral cavity.

In *Hemirhamphus unifasciatus* the mouth appears superior, but it is more truly horizontal, the appearance being produced by the great prolongation of the mandible. This species has the maxillary valve but little smaller than the mandibular.

Pomolobus pseudoharengus affords a very characteristic example of the development of the mandibular valve. The mouth being very oblique and narrow, the mandibular valve is very deep and "baggy." (Fig. 8.)

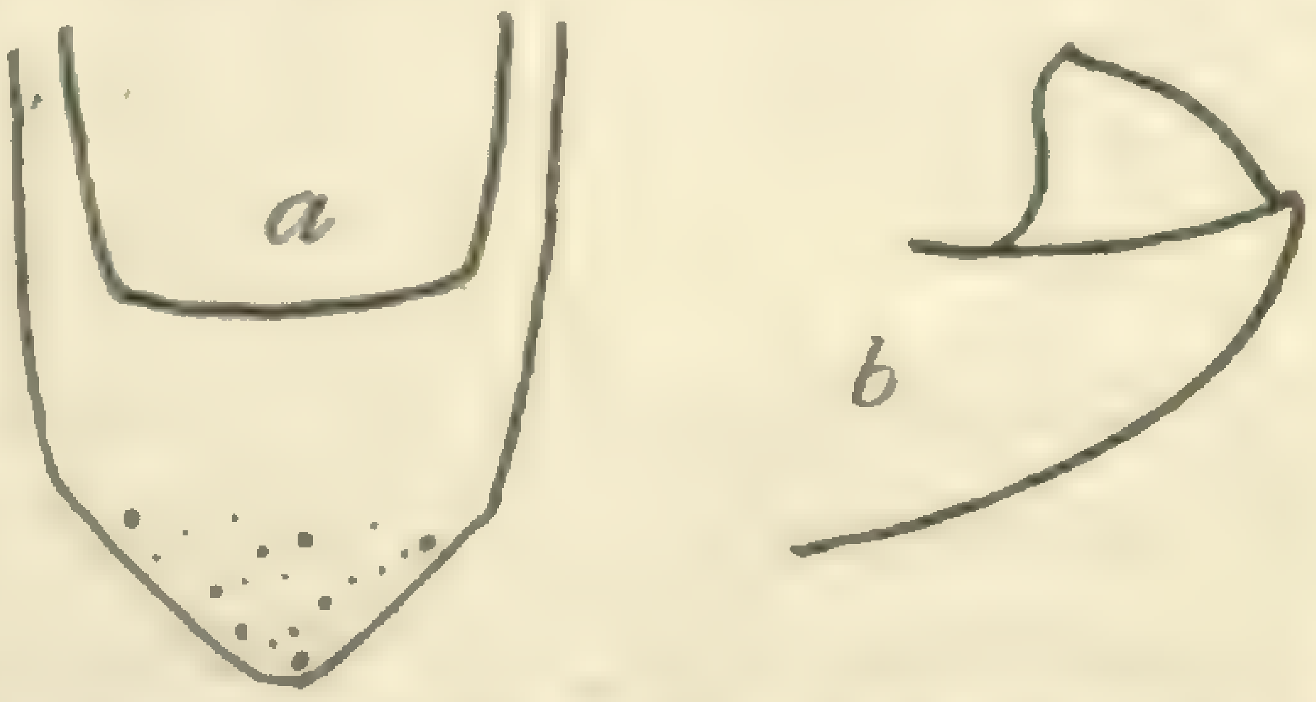

Fig. 8.— Mandibular V of *P. pseudoharengus*. *a*, from above; *b*, from the side.

In *Chilomycterus schœpfi* the valves are crescentic, the mandibular valve being four times the width of the maxillary valve. The valves are covered with coarse papillæ. They entirely close the mouth when the jaws are at full stretch, which has been noted in no other species.

A good example of deep valves is found in *Oncorhynchus nerka*, a salmon. In this fish the jaws are hooked, long and somewhat compressed. If the valves were narrow, there would be a long, free margin. Consequently the valves would have to be very heavy to resist the outward pressure from within against the unsupported margins. As it is, the free edges lie far back in the mouth, their length is much reduced and the surface of the valve, which is far better able to stand the strain, increased and hung in a better position for resistance between the bones of the jaws. (Fig. 9.)

The valves of predacious fishes seem to be the heavier and more strengthened by muscular thickenings. This may be because the feeding habits of such fish would be liable to injure the more delicate membranes.

The valves vary widely in different genera and in different species of the same genus. The generic variation depends on general shape, size and appearance; the specific on papillæ, muscular thickenings and pigment. The general type of a family, notwithstanding, is very characteristic, except, perhaps in the minnows, in some of which the papillæ form valve occurs. By general type, the general appearance is meant; not the crescentic or U-types only. Individual variation seems comparatively slight and generally resulting from injury. If one individual shows a certain arrangement of pigment, papillæ, and central thickening, it will, so far as it has been possible to ascertain, be found in the rest of the species and nowhere else. For convenience of comparison and explanation the writer has, where enough species and specimens were available, arranged results in synoptical form.

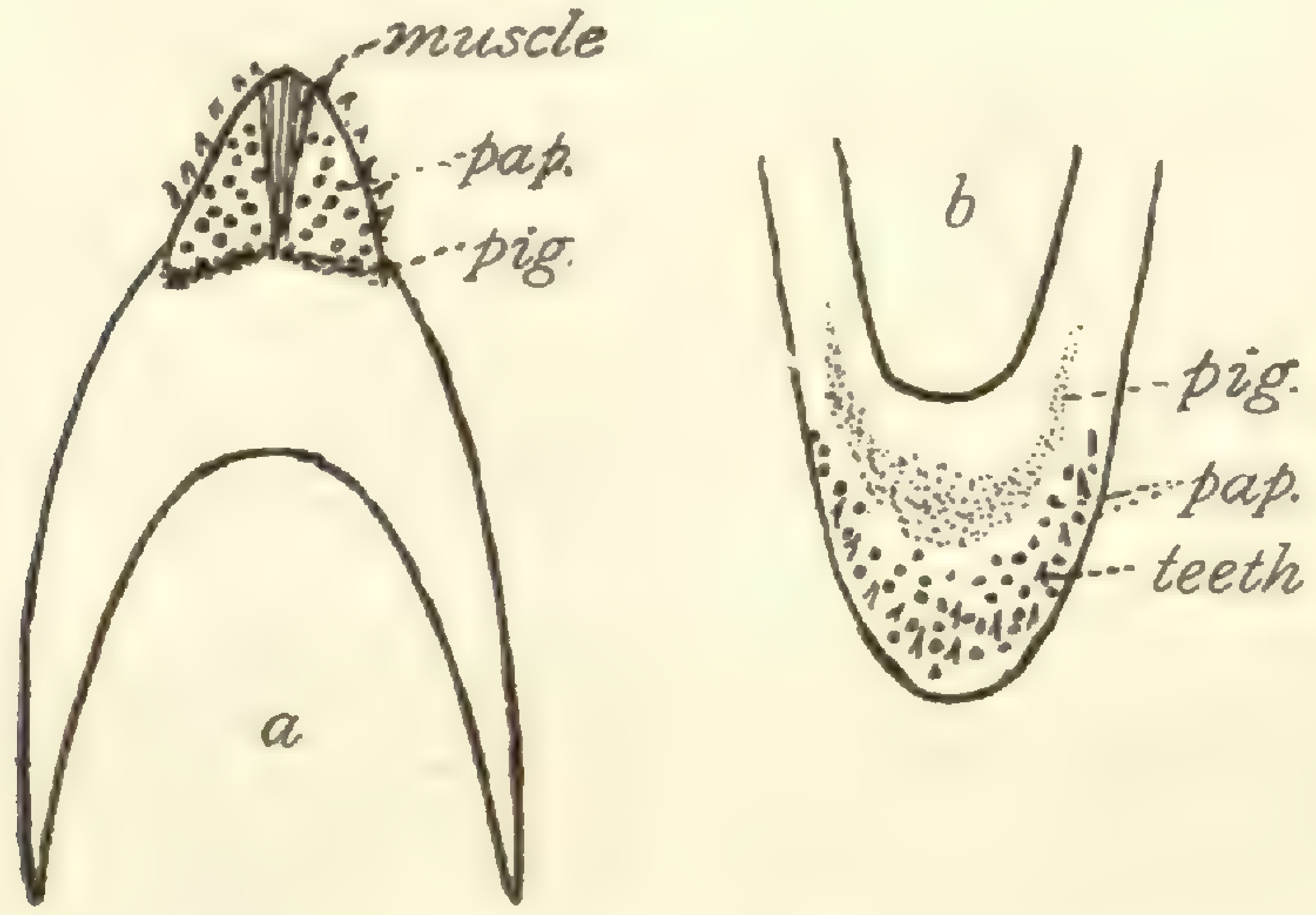

FIG. 9.—Valves of *O. nerka*. *a*, maxillary; *C*, mandibular.

The writer desires to thank Dr. Burt G. Wilder and Dr. H. D. Reed for valuable hints and use of specimens and, more especially, for their kind interest and encouragement.

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CATOSTOMIDÆ.

A. Papillæ present.

B. Small papillæ in fold-like rows over whole valve *Erimyzon sucetta*

BB. Papillæ not in fold-like rows.

C. Papillæ on proximal half[1] of valve *Catostomus macrocheilus*

CC. Papillæ over whole valve.

D. Papillæ crowded over whole valve; distinct, rounded, not so large as those on lips . . . *Catostomus catostomus*

DD. Papillæ less crowded in distal[2] half or in a circular mesal spot.

E. Circular mesal spot where papillæ are flattened, small and well separated . . *Catostomus nigricans*

EE. No such spot. Proximal papillæ about size of those on lips and in several rows. Distal papillæ less crowded, flatter, rather elongate *Catostomus commersonii*

AA. Papillæ absent.

F. Small thickenings, perpendicular in direction, resembling long, low papillæ in appearance . . . . . *Moxostoma macrolepidotum*

SILURIDÆ.

A. Papillæ on both valves.

B. Thickenings triangular and in Mand. V.

C. Thickening erect-triangular, (apex toward free edge) *Amiurus vulgaris*

CC. Thickening inverted-triangular, apex toward tooth pads.

D. Pigment on thickening and spreading in a crescent through the valve on either side . *Noturus gyrinus*

DD. No pigment in either valve . . . *Noturus miurus*

BB. Thickening in Max. V. and not triangular.

E. Thickening a vertical rod. Papillæ on Mand. V. larger and closer set than those on Max. V. . . *Amiurus nebulosis*

EE. Thickening not a vertical rod.

F. Thickening shaped like a sphere with a rod running through it parallel to the free edge *Amiurus natalis* (Fig. 4, *j*.)

FF. Thickening spherical, barely touching attachment and covering ⅔ the width of the valve. Papillæ so small that the valves at first appear smooth, on proximal ⅔ of the Max. V. sparsely scattered on Mand. V. *Ictalurus punctatus*

[1] Proximal, — near or toward the attachment.

[2] Distal, — away from the attachment.

AA. Papillæ on Mand. V. only.
Central muscular thickening passing between tooth pads *Noturus flavus*

CLUPEIDÆ.

A. Max. V. not attached mesally . . . . *Clupea harengus*

AA. Max. V. attached mesally.

B. Attached on one perpendicular median line.

C. Mand. V. a crescent, wide; the distal two thirds thin and delicate, no pigment . . . . . . *Dorosoma cepedianum*

CC. Mand. V. a horseshoe with pointed ends and the free margin rather squared off at the apex of the curve not perfectly curved like the attachment. Valve much wider at apical part of curve than on sides, (Fig. 2, *s*) *Opistheoma oglinum*

BB. Max. V. attached mesally on two lines. (Fig. *a. b.*)

D. Attachment V-shape. (Fig. 3, *a.*) *Clupea pseudoharengus*

DD. Attachment in parallel lines, margin between ends of these lines free. (Fig. 3 *b.*) . . . . . *Clupea æstivalis*

PERCADÆ.

A. Thickening in Max. V., a three quarters circle flattened against attachment and covering most of width of valve . . *Perca americanum*

AA. No thickening.

B. Papillæ and pigment . . . . *Hadropterus aspro*

BB. No pigment.

C. . . . . *Boleosoma nigrum*

CC. . . . . *Etheostoma caprodes*

CENTRARCHIDÆ.

A. Max. V. extending between tooth pads.

B. Papillæ in perpendicular rows on either or both valves.

C. Rows ridge-like (or fold-like).

D. Ridge-like rows on both valves . *Ambloplytes rupestris*

DD. Ridge-like rows on Mand. V. only
Pigment spots on the papillæ . . *Micropterus salmoides*

CC. Papillæ in rows on Mand. V. but not close enough to give ridged appearance. Slight thickenings in V. under the rows of papillæ. Clear margin . *Eupomotus gibbosus*

BB. Papillæ not in perpendicular rows.

E. Papillæ numerous on one or both valves.

F. Papillæ very large, flat and crowded on both valves, giving tesselated appearance, and extending between tooth pads . . . . *Apomotus punctatus*

F.F. Papillæ on Max. V. rather flat, medium size, crowded but not giving the appearance of those in F; a few pigment spots at meson; mesal fold *extending but slightly* between tooth pads.

Mand. V. covered with fine rounded papillæ little crowded, pigment in proximal half. . *E. auritus*

EE. Papillæ few.

G. A few large papillæ on Mand. V. along attachment; central thickening extends through tooth pad and half way to margin; well pigmented. Papillæ in Max. V. fine and well separated *Chænobrytes gulosis*

GG. No papillæ in Mand. V. Mand. V. well pigmented at base, and meson quite black. Max V. well pigmented, especially between tooth pads. Papillæ few and small . . . . *Pomoxis sparoides*

AA. Max. V. not extending between tooth-pads.

H. Papillæ in vertical, fold-like rows . . . . *Apomotus pallidus*

HH. Papillæ not in vertical, fold-like rows.

I. Papillæ of Mand. V. very few and flat, hard to see. Those of Max. V. blunt setiform. Mand. V. well pigmented on proximal half . . . . *Micropterus dolomieu*

II. Max. V. with fine, rounded, evenly distributed papillæ and slight mesal thickening. Mand. V. with fewer and somewhat larger papillæ; a few pigment spots on base at meson extending through tooth-pads *Eupomotus holbrooki*

ARGENTINIDÆ.

Valves crescentic; no papillæ; mandibular valve somewhat the larger.

A. Mesal thickening on mandibular valve circular in shape and placed against attachment of valve, covering about ½ the width of the valve. Central third of maxillary and proximal half of mandibular valve pigmented . . . . *Osmerus mordax*

AA. No mesal thickening.

Pigment spots near attachment of mandibular valve, few and variable . . . . *Hypomesus pretiosus*

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IN THEIR WIDEST SENSE

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THE

AMERICAN NATURALIST.

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BREEDING HABITS OF CRAYFISH.

E. A. ANDREWS.

Of the breeding habits of the European crayfish much is known, but this is not the case with the American species. The easy assumption that the habits here were essentially identical with those there, has been, possibly, one reason why so little has been put on record regarding our American forms. That there are, however, some considerable differences will appear from the following notes made upon that common species *Cambarus affinis* in 1894 and 1900–1903. Though these observations were made upon individuals kept in confinement in the Biological Laboratory, they may, for the most part, be taken as a guide to what is to be expected from field observations, which still remain much to be desired.

Sex ratio.— The specimens used were taken from the Potomac River in Maryland and when attention was given to the ratio of the sexes it was found that one lot in March 15, 1901, contained 26 females and 14 males while another lot, April 20, 1903, contained 39 females and 14 males. While this shows a marked predominance of females over males at those periods and at that locality it is not general, for a lot of eighty of the same species taken in October, 1903, from a pond in Baltimore, con-

tained 41 females and 39 males. Even where the females are more abundant there is no probability of the eggs going without fertilization since it was found that one male unites with several females.

Time of sexual union.— When specimens were taken in February and put into tanks some unions occurred at once while others were deferred till March. When the sexes were kept separate till March 6 and then put into one tank, unions took place March 6, 7, 8, 9, 10 and 11. After that there were occasional unions, especially of the younger and smaller animals, up to April 2. Besides these observed unions in February, March and April it would seem that there is an Autumnal pairing, in place of or in addition to the Spring pairing. Several small specimens reared from eggs laid in the Spring were found to pair early in October of the same year; while at that same time pairs of larger size were taken in a pond in Baltimore. Moreover specimens from Washington, D. C., in 1894, in November, were seen to pair as soon as they were put into a shallow dish.

Description of sexual union.— The union of the sexes in *C. affinis* was first observed in 1894, and briefly described in the *American Naturalist* in 1895. The same phenomena have been repeatedly witnessed in successive years and there is no doubt that in this species of crayfish the sperm is transferred from the male to an external seminal receptacle upon the female where it is stored up till the time that the eggs are laid. There is no copulation or use of intromittent organs such as takes place in the crabs; nor on the other hand is there any such vague attachment of spermatophores as has been described in the European crayfish, Astacus.

In captivity the union lasts from two to ten hours and either the male or the female may repeat the process with other individuals.

When a female is put into a dish in which a male has been kept till he is accustomed to it he soon seems aware of the presence of the female and does not act as he does when only males are introduced. The preliminary steps toward union are soon taken. The male advances with ready claws and seizes the female, sometimes gently. The female retreats or, when

seized, often struggles to escape. Despite these struggles the male holding the female with one of his claws fastened to her antenna or to any projecting part of her head eventually succeeds in turning the female over to lie upon her dorsal surface: if there is no struggle the same result follows more directly and methodically. When the female is turned over the male stands over her ventral surface and later transfers the sperm to the receptacle.

When the first seizure is not effective in leading to a ready turning of the female the male exhibits considerable skill and shows something like intelligence in commanding the new circumstances. Two cases were seen in which the male mounted upon the back of the female and seized her claws as is usual after turning the female over, though in this case turning had not been accomplished. In this unusual position the male attempted to adjust the sperm-transferring appendages to the female and then desisted: then the long antennæ of the male were bent down strongly against the dorsal side of the thorax of the female. In one case the exopodites of the third maxilliped were also used in feeling the female. After getting some information, apparently, by the use of these sense organs, the male proceeded to turn the female over and finally continued a normal sperm transfer. In this turning over the male had to deal with the problem of revolving the female through 180° while under his body and starting with his right claw holding her right claw and his left holding her left so that finally his right held her left and his left her right. In accomplishing this feat the male first removed his left claw from the left claws of the female and with it seized her rostrum and adjacent head region: he then turned the female about 90° so that she lay upon her left side while he stood over her right side. Next the right claw released the female's right claws and seized her left claws. He was now able to turn the female through 90° on to her dorsal surface. Then he transferred his left claw from her rostrum to hold all her three right claws. After that the usual union could take place and ten minutes later sperm was transferred and union continued for some hours.

Usually as soon as the male has thrown the female upon her

back he seizes all her clawed legs with his two large claws, holding the three left ones of the female with his one right claw and the three right ones of the female with his left. He then moves forward over the supine female to the position indicated in Fig. 1. From this figure it is evident that the two crayfish are accu-

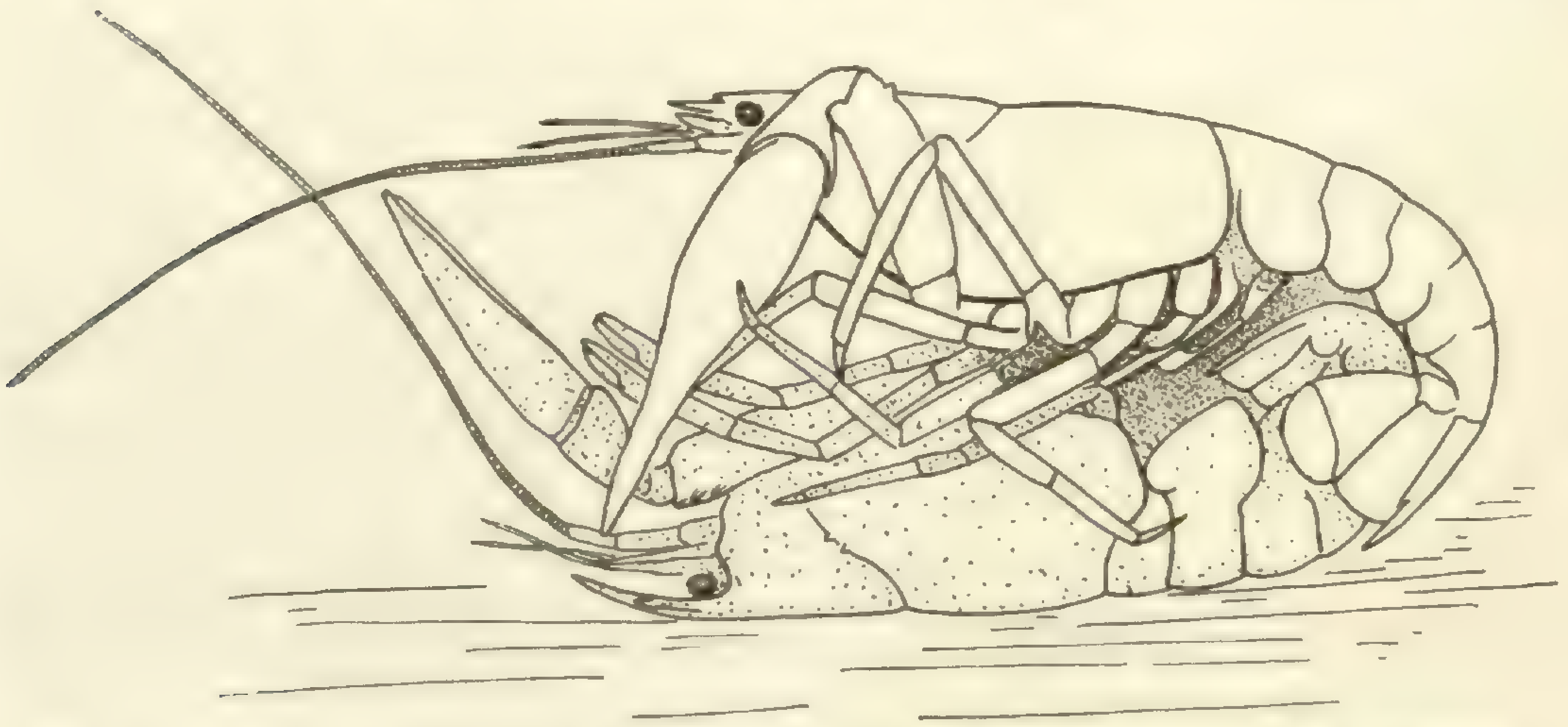

Fig. 1.— Male holding female and with fifth leg supporting abdominal appendages that are about to transfer sperm to the annulus of the female. × ½ diameter.

rately and closely adjusted to one another; not only does the male hold all the claws of the female, but his abdomen is tightly bent around that of the female which is closely coiled up under the male. While all the five right legs of the female may be seen, there appear to be but four legs of the male's set of five left legs. The base only of the male's fifth leg is shown; posterior to this are the peculiar long male pleopods, or appendages of the first abdominal segment and of the second abdominal segment. These four appendages are elevated at an angle of about 45° and point toward the ventral surface of the thorax of the female, forward and downward. A view of the right side of the pair would, however, show the left fifth leg of the male projecting outward and backward between the fourth and fifth legs of that right side.

The explanation of this peculiar arrangement is found in a habit of the male which seems necessary for the accomplishment of sperm transfer and is a very instructive example of mechanical adjustment amongst several rigid calcified organs. After the male has come forward over the supine female there is a period of ten to twenty minutes of apparent inaction before

the next move which is as follows: the male rises up away from the female, but still holding all her claws, and deliberately passes one of his fifth legs across under his body so that it projects from the other side. When the male again settles down against the female it is found that the pleopods have the position shown in the figure, whereas before this move they had the normal position, being directed forward, horizontally under the thorax of the male.

It is this forced and remarkable position of the fifth leg which secures the necessary elevation of the male pleopods. These pleopods might be compared to the blade of a pen knife half open and tending to shut up into the handle when pressure is exerted against the tip: and as such a blade might be held in position by a pencil placed across between the blade and the handle and held there, so the pleopods are held in position by the crossed leg which lies anterior to them and between them and the thorax of the male. All these parts are firm and rigid and the pleopods articulate only where they hinge to the abdomen. As the male draws himself down with force against the female the pleopods are so held by the above device, that their tips enter the annulus of the female and the pressure so exerted would tend to shut them down into their resting position, but this is opposed by the fifth leg which blocks the pleopods firmly. That there is force exerted by the tips of the pleopods against the annulus was shown in the case of a female that had been reared from the egg in the Laboratory and when put with a male in April of her second year was covered by a dark blackish deposit after wintering. It was soon found that in union with the male the edges of the opening of the annulus had been scraped clean of the dark deposit and stood out conspicuously against the rest of the dark exo-skeleton.

Though the male always uses one of his fifth legs as an apparently necessary secondary sexual organ it is not always the right or the left; males were seen with right and others with left legs so used. Whether the use of right or left is fixed for each male by circumstances or whether it is a matter of chance or whether inherent in the structure of each male was not determined, but a student who kept many crayfish and sought to

determine this point reported to me that one male was seen to use the same leg on one side, in several successive unions with different females.

In one case the fifth leg was seen to project between the third and fourth legs of the opposite side instead of between the fourth and fifth as is the rule. Possibly this may have been in connection with some difference in size between the female and male. . Though the two pairing are about the same size there is often considerable difference in length and to secure accurate interadjustment of such rigid bodies with so many protuberances and pairs of appendages is no small problem. To solve it the male at times relaxes his abdomen and moves forward over the female and when finally the tips of the pleopods have been introduced into the annulus the male again envelopes the end of the abdomen of the female and firmly holds it as in the hollow of a hand. The persistent union of the two is made more complete by the use of the hooks found on the legs of the males of this and some other species of Cambarus ; apparently these fasten the male so that the abdominal pressure exerted down the pleopods against the annulus does not react and push the male upward away from the female. In *C. affinis* there is one of these hooks or spines on the third segment of each third walking leg and the male fastens these two hooks into the base of the fourth legs of the female. In the above figures the male has raised the third left leg so that the hook is free and far from its proper socket. When lowered into place the hook depresses the soft membrane that forms the external aspect of the basal segment and thus a temporary socket is formed. The outer ventral edge of this socket is bounded by the stiff calcified ridges that help form the hinge between the first and second segments and it is against this rigid rim that the spine of the male's leg catches. The use of these male hooks as secondary sexual organs is thus established and we may expect to find that in those species of cambarus in which more than one pair of legs are provided with such hooks, that there will be a corresponding increase in complexity of the adjustments of sexual union.

The union of the male and female is now so firm that they cannot be readily separated, and if thrown into actively boiling

water the two may be fixed in almost normal positions and serve to make most excellent museum preparations.[1]

Bound together in this way the transfer of sperm from male to female takes place during several hours. Since the crayfish may now be roughly handled or transferred from one dish to another there is little difficulty in observing how the sperm-transfer is effected and a lens may be used without causing the union to cease. The terminal part of the vas deferens of the male, on each side, is found in this period of union to protrude horizontally into the water from the base of each fifth leg as a short, soft, bent tube of translucent appearance. This organ fits exactly into the beginning of the long groove that passes down the first male pleopod, right or left. These pleopods are in fact massive, calcified and rigid tools, each with a deep sinuous groove along it that is seen to lead the sperm from the above ending of the vas deferens down to the tip of the pleopod. The specialized, sharp tips of these organs are inserted into the annulus. The sperm seen to issue from the vas deferens tube glides down the groove of the pleopod to the annulus in the form of long, macaroni-like cords. Microscopic examination of these cords reveals a central axis of real sperm made up almost entirely of the sperm cells and an outer tubular case comparable to soft macaroni. During this transfer of sperm the tip of each pleopod of the second pair is closely applied to the pleopod anterior to it, but no observation was made upon the mode of action of these second pleopods. Each of them has terminal filaments that may well be sensory and also a peculiar, soft, somewhat triangular "spoon" or scoop that fits nicely against the groove of the first pleopod. It would seem that the second pleopods may act to convey sensory impressions and to protect and guide the sperm masses which were found not to go astray but to be in some way retained in the grooves of the first pleopods and forced on into the annulus, probably with the guidance and direction of the second pleopods.

Probably both sides of the body in the male are active at the

[1] The same method may be used to advantage for museum specimens of females "in berry" etc., since the coagulation of the liver, etc., lessens the solubility of substances that ordinarily discolor the alcohol.

same time in transferring sperm, but this was not directly observed. During the whole process of union the male is in a state of excitement while the female is quite the reverse, as far as could be judged. The action of the male in turning and adjusting the female is greatly assisted by the state of passivity simulating death that overtakes her soon after being seized by the male. This inertia of the female extends even to the respiratory movements, which seem absent in strong contrast to the condition in the male. The female seems to be dead and the only signs of the continuance of life that were seen were the movements of the eye-stalks in cases where the efforts of the male led to his claws coming against the eyes and, at times, a slight convulsive tremor in the abdomen, possibly connected with sperm transfer. The very small first pair of abdominal appendages which lie often against the annulus and have no probable use unless it be in connection with the phenomena of union, may convey sensory stimuli and occasion the above abdominal contractions. On the other hand the male is in a strongly excited state during the entire period of union: when the struggle and turning have ceased there are still quick vibrations of the anterior maxillipeds and strong currents of water thrown out from the gill chamber as well as the long continued contractions of the limb and abdominal muscles and probably those of the internal male organs. The process terminates when the male moving backward and rising up crosses his fifth leg back again under him into its own side. He then releases the female.

The annulus.— Thus the result of union of male and female is the storing up of sperm within the annulus or sperm receptacle of the female. This is in strong contrast to what has been described as taking place in the European crayfish, Astacus, which has no annulus; for French observers state that the male distributes sperm masses, or spermatophores, over large areas of the under side of the female. On the other hand in the American lobster a transfer like that in Cambarus doubtless takes place since Bumpus discovered the sperm-containing receptacle upon the female.

The structure which serves in the lobster to hold sperm is,

however, apparently not homologous with the annulus of Cambarus but is different in position and construction. Whether there may not be some kind of receptacle in Astacus, as some appearances there would suggest, something more like the receptacle of the lobster, is a possibility that needs future consideration. It is well known that the annulus differs in many species of Cambarus, and now that we know its use as a sperm receiver we may expect to find some of these specific differences have their uses in the processes of union. The male pleopods are also characteristically and often remarkably different in various species of Cambarus, and these differences may find their explanations in their uses with different styles of annuli.

In *C. affinis* the annulus may be described as a calcified region on the ventral side of the thorax between the sterna of the somites bearing the fourth and the fifth legs. The sternum of the former somite is a wide plate, concave across the middle line and rising up at its edges right and left as two high plates that diverge posteriorly and stand close against the bases of the legs. The sternum of the latter somite is a transverse band enlarging at its ends against the right and left fifth legs and bearing at its middle a transversely elongated rounded elevation. All these parts are hard and calcified. The annulus fills all the space between the above sternal plates and thus lies across the ventral line at the interval between the fourth and the fifth legs. It is close against the sternum anterior to it and may be moved slightly as if hung to it by a stiff hinge.

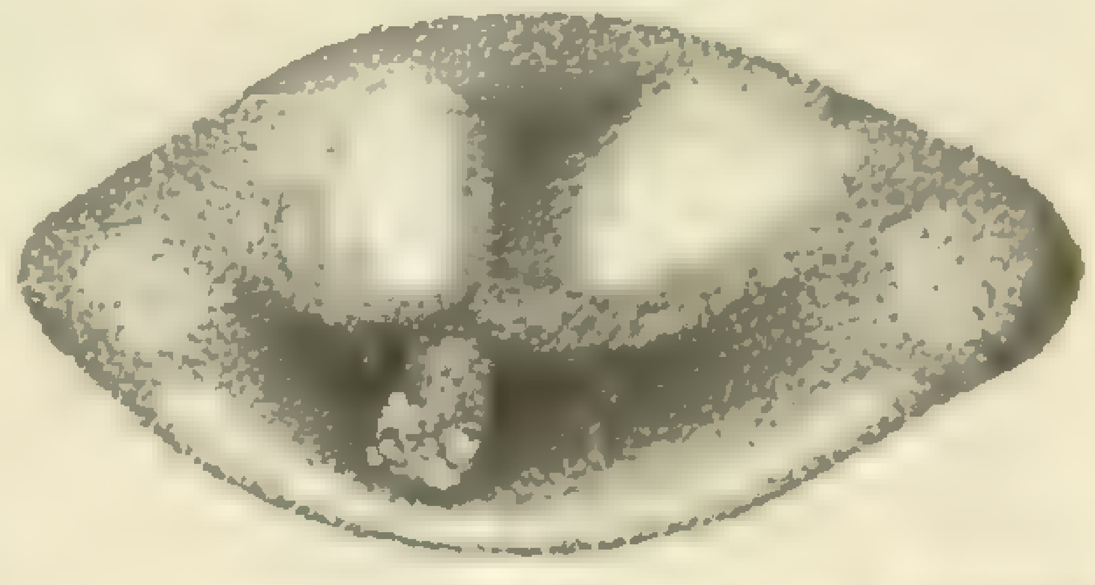

FIG. 2.— Annulus with projecting sperm-plug. × 8 diameters.

In shape the annulus, Fig. 2, is a transverse and elongated ellipse with pointed ends right and left. It is a calcified plate with two elevations, or hills, of varying size and shape near the middle — one right, the other left. Between these elevations is a longitudinal groove and at the bottom of the posterior part of this groove is a narrow chink into which a fine instrument may be forced. This chink opens posteriorly into a deep groove or valley that runs from right to left across the major part of the annulus. This big groove is just posterior to

the long axis of the annulus and anteriorly it is overhung, somewhat, by the two hills, while posteriorly it is bounded by an elevated lip or transverse ridge that forms the posterior edge of the annulus and sometimes shows a faint crack in it as if made of right and left halves welded together.

Though the hills are right and left the median slope of one extends across the median line of the body of the crayfish so that the chink between the hills is always asymmetrically placed, sometimes on the right and sometimes on the left. In forty-one females, all but two of which were young, probably but four months old, examined in October, only three cases were found in which the chink was on the left side; in the thirty-eight other females it was upon the right side.

In four still younger females, 32–40 mm. long, the annulus was found less well developed and with but slight transverse groove.

Sections of this organ show that the chink opens into a small rounded pouch or sac which as seen from a dorsal view projects upward as a small, curved ridge. Its walls are stiffly calcified cuticle and no opening could be found excepting the external chink above mentioned. This cavity of the annulus serves as the seminal receptacle, but it is only a small, specialized pit in the external cuticle or exo-skeleton.

After sexual union the female shows a white plug of waxy substance projecting from the chink and filling up the transverse groove at that point as indicated in Fig. 2. This plug is necessarily excentric, generally upon the right side, but in some females upon the left side. It is the surplus sperm envelope or macaroni-like case that came down the pleopod groove and was forced into the chink of the annulus. This plug may remain for weeks, but it disappears some time after the eggs are laid. It may thus be used as evidence of foregoing union for a much greater time than the vaginal plug of some rodents can be. Examining the contents of the cavity of the annulus when the plug is in evidence we find it full of a similar compact paste-like material that may be quite hard and has the form of a tubular sheath around a granular mass that proves to be the peculiar sperm cells of the crayfish. The sperm in this sperm receptacle

is in very small amount as compared with the amount produced by one male or with the great mass of eggs to be fertilized, but the actual number of sperm cells is quite large and that they are numerous enough to fertilize all the eggs seems certain though not actually demonstrated. As a fact when females were isolated as soon as union had taken place and kept apart from males till eggs were laid these eggs developed as if fertilized. No sperm was ever seen to be deposited by the male upon other parts of the female than the annulus and if it were not protected as in the annulus it is difficult to see how it could long survive exposure to water which quickly destroys the sperm cells. The laying of eggs, however, may not occur for some weeks after union.

Again, in one case in which the annulus was removed from a female just before laying, the eggs were deposited with normal secretions and habits and though the female was left undisturbed for five days the eggs then appeared shrunken and abnormal, to the naked eye. Twenty-four days later there was only a mass of mouldy dead eggs left on the female. Though there were some cases in which normal females lost most of their eggs by death and fungus yet the above eggs were thought to be all bad from an early date and it is probable they were not fertilized, in the absence of the annulus.

On the whole the evidence seems strongly to favor the view that the sperm received into the annulus in union is the sperm which later fertilizes the eggs. In fact it is possible that sperm taken in antumnal unions may be used for the eggs laid the following spring. Experiments to test this are not yet completed.

Mortality. — The crayfish kept in the laboratory were not fed till after they had laid eggs; then they ate meat, raw and cooked, raw hen's eggs, and pieces of earth worms, as well as Chara and Hydrodictyon. After sexual union many died and it was found that the males died in larger numbers than did the females: thus in one lot seventeen died within two weeks of union in March, and thirteen of those were males and only four females. In several cases the males died within a few hours after union.

Date of laying. — After union there is quite a long period

before the eggs are laid : this period is often some weeks. When about 100 males and females were put together March 6–11 the first eggs were laid March 24th, while other females laid from then on to April 15th, though those laid after the first of April were probably unduly retarded by various artificial influences. That March is the normal time of laying for this species and at the Maryland station on the Potomac whence these specimens came is shown by the fact that 39 females taken there April 20th, 1903, all bore eggs in late stages of development that were almost the same as the various stages then present in the eggs laid in March by the previously captured specimens.

Preparation for laying. — The females tend to secrete them-

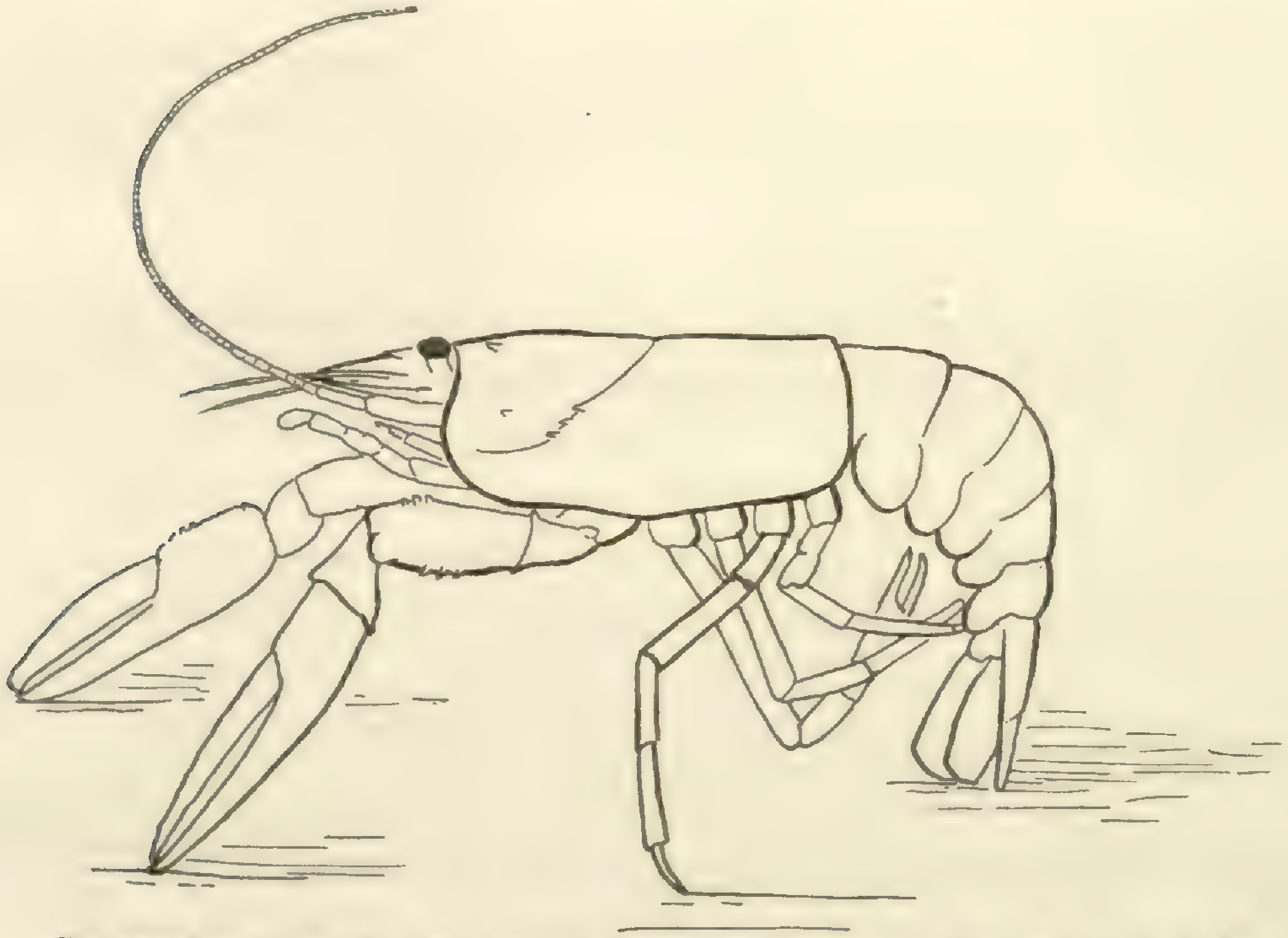

FIG. 3.— Female standing like a tripod and cleaning abdomen with small claws. × $\frac{1}{3}$.

selves in dark corners and four or five days before laying they are noticeably excitable, an approaching object causes them to raise their claws and to assume the defensive in a much more active way than was previously the case.

These days are also taken up with great and peculiar activity upon the part of the female resulting in a very thorough cleaning of the ventral side of the abdomen. No matter how darkly discolored the exo-skeleton may have become during the winter it is now made white and clean over the under side which then comes to contrast strongly with the remaining dark exterior.

The process of cleaning was observed in a number of cases and always ran the same course. Though the female is now so alert that it is difficult to catch her in the act of cleaning yet the attitude assumed is most noticeable when seen. As indicated in Fig. 3 the body is raised high up from the usual crouching, crawling position and stands like a tripod supported above the bottom of the aquarium upon the two outspread large claws in front and the oddly down-bent abdomen behind. The other legs aid but little in support of the body and are concerned with the cleaning of the abdomen. The fifth legs, and at times the second and third also, were seen to be thrust back under the abdomen and there carefully and patiently used to remove

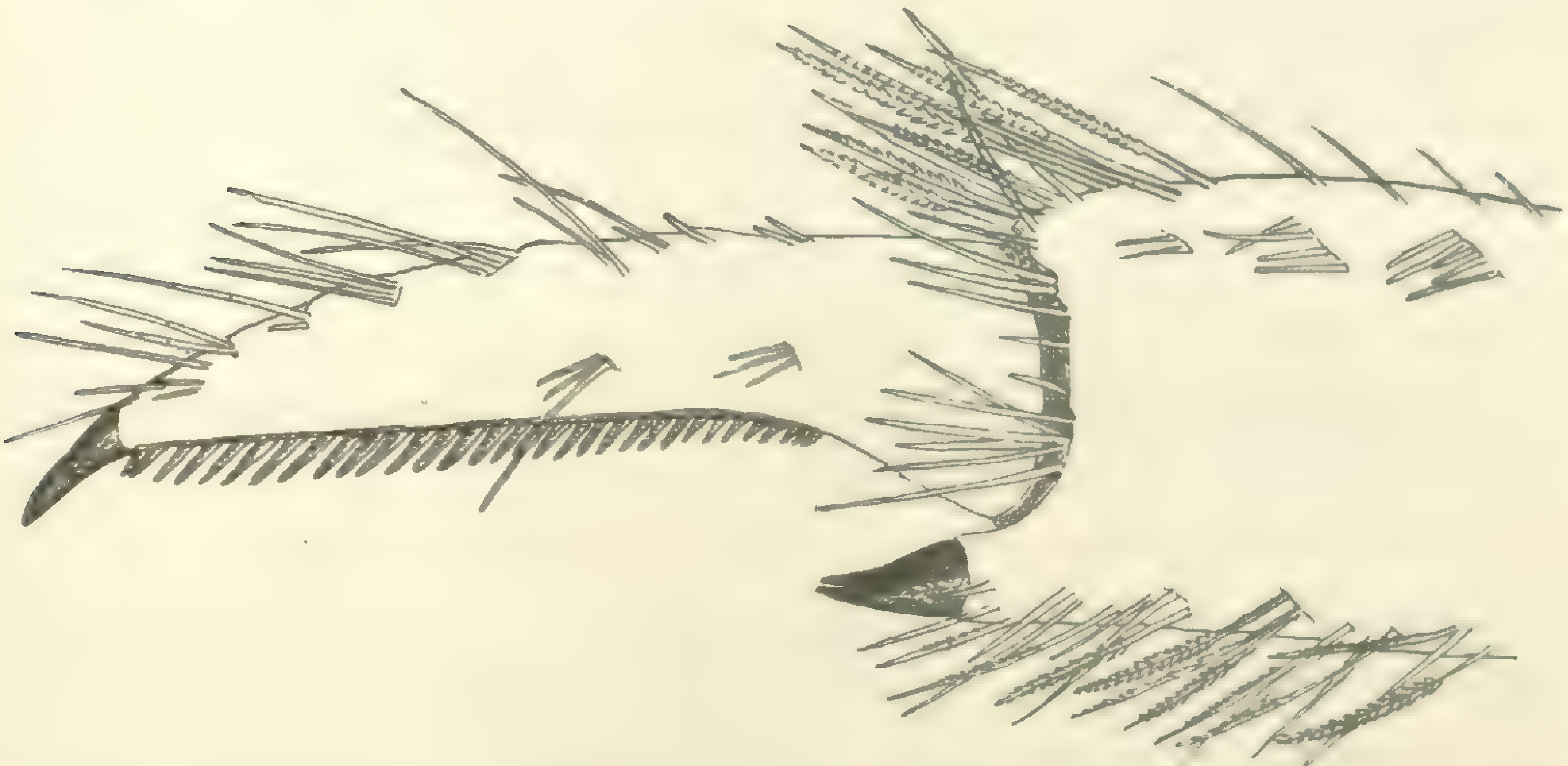

FIG. 4.—Comb and picks on end of fifth leg; used by female to clean abdomen before laying. × 20.

all the dirt from the entire under surface including the pleopods. Even the numerous long, plumose hairs on the pleopods lose their covering of dark "dirt," and the transformation wrought in the appearance of the whole under side of the abdomen is so great that one would suppose the crayfish had cast its shell and wore an entirely new one.

The ends of the fifth legs are shoved against the pleopods and other parts of the abdomen with considerable force but it is only slowly that they accomplish perceptible cleaning. On examining the tips of these legs we find they seem especially well fit for such cleaning work. As indicated in Fig. 4 the terminal segment is like a strong comb, as it has a series of spines

along one free edge. At one of the angles of the penultimate segment there is a group of strong picks that look like the horny tips at the ends of legs. In fact these two picks are born upon a truncated process that suggests a homology with the finger of the chelate legs, that process of the penultimate segment which apposes the last segment to form the claw; and we might regard this fifth leg as having lost, or not yet acquired, a perfect claw. The penultimate segment also bears beautifully serrated hairs, as indicated in the figure, recalling the appearance of some setæ of annelids. That these tufts of serrated hairs may serve as scouring brushes seems not improbable. We would then have a double pick to loosen dirt, a stiff comb and a brush with saw-tooth hairs to accomplish the cleaning.

The fourth leg has the same structure and though it was not seen in use it may well take part in cleaning. The second and third legs bear well developed claws and these were seen slowly plucking at the encrusted abdominal surface. As elsewhere shown[1] these claws are well fitted for cleaning as they can pick off objects and are provided with a long row of flat, serrated plates on each limb of the forceps that should serve excellently in cleaning the pleopods.

Time of laying. — In confinement the crayfish deposited their eggs at night time with few exceptions; only one among thirty-two laid eggs in the day time. Yet it was found possible to force the laying of eggs in the day time by keeping the female every night in barely enough running water to moisten the ventral surface of the body and with no opportunity for the normal submergence. When returned to deeper water in the day time eggs were finally laid, at noon, upon the third day of such treatment.

Laying. — The females were easily disturbed and never laid when under observation so that the actual emission of eggs was not seen but the following facts were observed just before and just after the actual laying. A short time before laying the female is sometimes found lying upon her back waving the abdominal appendages back and forth in a rhythm of about

[1] *Biol. Bull.* Jan. 1904.

one second. The endopodites of the third maxillipeds and the anterior three pairs of legs are sometimes swung back and forth also. Finally a peculiar secretion is passed forth and the eggs are then laid. This secretion is furnished by the "cement glands" of the under side of the female and needs special notice. One of the things that make much for the clean appearance of the under side of the abdomen when the female is about to lay is the presence of large milk-white areas on the basal parts of both endopodites and exopodites of the sixth pair of abdominal appendages, forming very conspicuous white patches when the tail fan is expanded. The other pairs of pleopods are pretty uniformly milk white but the endopodites are more densely white and the glands in their terminal parts are somewhat segmentally arranged. The sternal plates between all six pairs of pleopods also stand out as milk white areas. Anterior to the abdomen the only milky gland areas are the sternal plate of the last somite, the annulus and the edges of the two flaring sternal plates anterior to the annulus. At other times of year these "cement gland" areas seem inactive or at all events inconspicuous. When a portion of one of the milk areas was removed from the tail fan or from any of the smaller pleopods it furnished, under pressure, a milky material which swelled up in water as a clear jelly containing minute spherules as seen under Zeiss 2. D. and as a somewhat milky glair as seen with the naked eye. When first pressed out from a piece of the glandular area the secretion also contains the minute spherules or droplets.

In one case a female was seen to stand with the body raised high above the bottom of the tank and to wave the pleopods back and forth while they gradually became covered with a clear slime or glair. Forty-five minutes later, at 1.15 p. m. the female was lying upon her back and all the eggs had passed out of the oviduct. The general appearance of this female that had just laid is indicated in Fig. 5. Lying upon the back with the limbs stiffly extended and no motion visible the creature seems dead unless the strongly bent abdomen suggest muscular contraction. Passing forward from the widely expanded tail fan is a faint film of slime or glair that

extends to the second legs and neighboring parts. Under this veil a few eggs may be seen not far from the oviduct but the great mass of eggs, several hundred, is concealed by the bent abdomen which encloses them somewhat as a nearly closed hand might a quantity of shot. The actual openings of the oviduct are concealed since the abdomen is bent to its utmost and the tail-fan is carried very far forward over the ventral surface of the thorax. Some slight tremors of globules in the glair near the openings of the oviduct suggested rhythmic contraction of the oviduct, about once a second, even after the

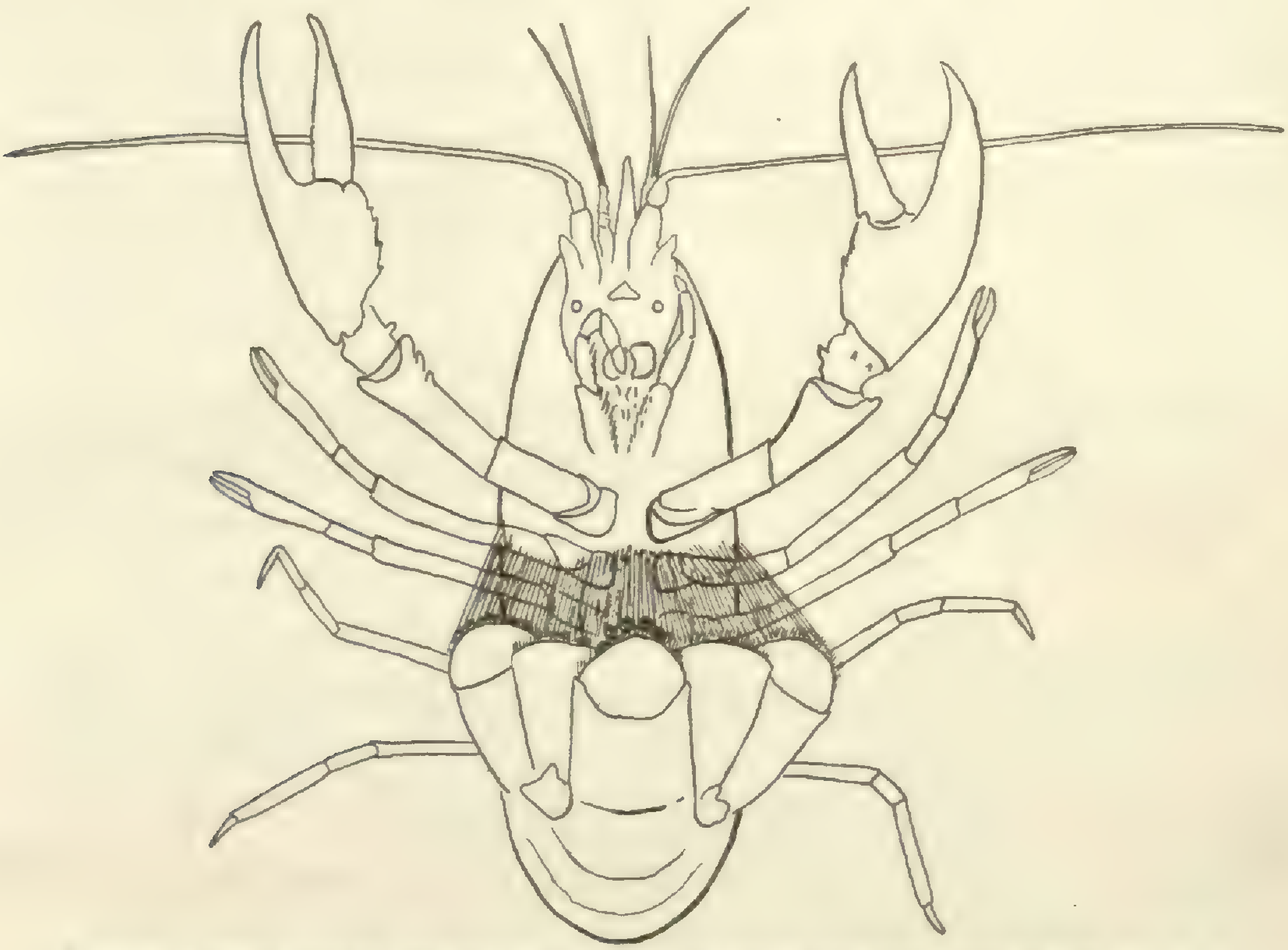

FIG. 5.—Female lying on back with legs held rigid and apron over eggs as they are being laid. × ½.

eggs had been laid. Gradually the abdomen relaxed somewhat and allowed more of the ventral surface to be seen; while most of the eggs lay in a mass enveloped by the abdomen, some of them still extended forward on to the thorax as a flat layer. After ten minutes there were some slight movements of the legs and then of the second maxillipeds also. Six minutes later the legs moved more actively and a minute later the crayfish turned itself over on to its ventral side, though this was not easily done in a smooth glass dish.

The eggs must have passed out of the oviducts in a short space of time and have been received into the basket formed by the bent up abdomen, a basket full of glair that would protect the eggs from contact with the water. That this glairy substance is the secretion of milk-white cement gland areas seems certain ; when the material about the eggs is examined under the microscope it contains droplets like those found in the secretion of the cement gland.

The probable mode of laying may be inferred from the above observations and from the following considerations. If we place a female crayfish upon her back and bend the abdomen forward over the thorax as far as possible we can see that if the eggs were forced out by the contractions of the oviducts they would issue in two streams from the mouths of the oviducts which are on the bases of the antepenultimate legs : they would then emerge into a median triangle-like depression formed by the thoracic sterna and this would form an inclined plane down which the eggs would flow into the basket formed by the abdomen, which is on a lower level. When first seen the eggs were very soft, apparently liquid and most easily deformed and indented yet coming rapidly back to a spheroidal shape, owing, partly at least, to the presence of a thin membrane. At first the eggs were not spherical but pear-shaped or elongated ; but when put into hardening liquids they took on a spherical form. When the female is lifted out of the water the soft eggs crowd together and have polyhedral shapes as if liquid, or plastic. In the position assumed by the female it would seem that gravitation acting upon the liquid eggs would bring them into the abdominal basket.

The female that has laid continues to hold the abdomen flexed and the eggs are contained in the basket of glair for some hours. As seen from the side such a female, Fig. 6, seems to have an apron of glair stretching from the second legs and that part of the thorax back to the expanded tail fan and somewhat bellied downward as time goes on. In this condition a remarkable rhythmic habit was observed in several females and regarded as a necessary element in the future success of the eggs. This performance lasts several hours and may be spoken of as : —

Turning.— It consists in a long series of changes in position from the right to the left : the female lies as if dead now on one side and now on the other. After lying a few minutes upon the right the female got back into the ventral position and in a minute or so turned on to the left side, remained there a few minutes and then went back to the ventral position for a minute or two, then to the right side and so on. The striking features in this set of habits are the inert state assumed while lying upon the sides and the great regularity and persistence of the alternating rhythm. The following example will show the details of this process as observed in female XXXII, April 15, 1903, from 1.35–

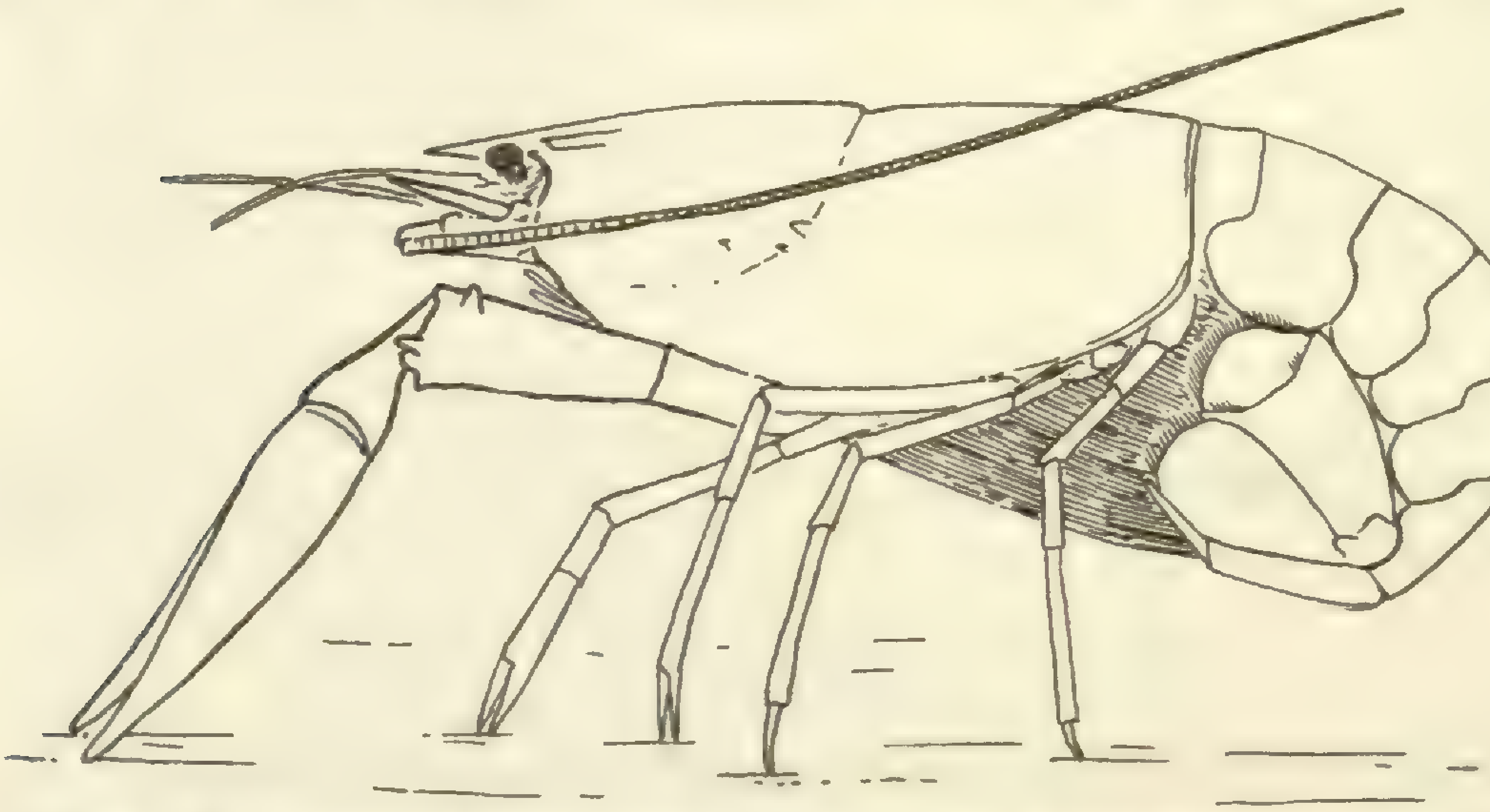

Fig. 6.— Female standing up after laying: apron connecting thorax and bent abdomen. × ½.

5.50 p. m. As shown in the table this female, as soon as the supine egg-laying position was given up, remained upon her ventral side for three minutes, as in Fig. 6, then turned and lay upon the right side for two minutes, then upon the left side for six minutes, then upon the ventral side for one minute, upon the right side for three minutes and so on.

V3,	R2,	Vo,	L6,	V1,	R3,	V1,	L4,	V2,	R2½,	V½,	L4
V1,	R4,	V1½,	L4½,	V½,	R3,	V½,	L4,	V1,	R2,	V3,	L6
V2,	R3,	V1,	L4,	V1½,	R3½,	V1,	L6,	V1½,	R3,	V2,	L4
V½,	R6,	Vo?,	L5,	V11×,	—	—	L3,	Vo,	R4,	V½,	L6½
V3,†	R4½,	V4,	L4,	V1,	R4½,	V1,	L6½,	V2½,	R5,	V1,	L6½
V1½,	R6½,	V1,	L6½,	V1,	R7½,	V1,	L5,	V2,	R7,	V½,	L5½
V2,	R8,	V1,	L5½,	V1,	R7½,	V1,	L4½,	V3,	R5½,	V	—

Observations were discontinued with the animal upon the ventral side at 5.50 p. m. In this long series there is only one break in the rhythm at the point marked x when after 51 minutes of turning in which there were ten alternations from right to left; the female then walked about the dish as if seeking some corner more retired than the one she finally returned to and remained in to make the following ten alternations. This walking away from the corner otherwise so closely kept accounts for the long interval of eleven minutes on the ventral side in place of the usual one of only one or two minutes; to it also may be due the break in the close sequence, the turning upon the left side when the right was the one to be expected; unless indeed we assume the time factor to be so dominant as to cause the female to go over to the left side after eleven minutes because that would have been time enough for, say, a ventral rest of 2 minutes, a right rest of 7½ and a left of 1½ which would bring the period around again to a left rest as next in order. At the point marked † the ventral time is abnormally lengthened as it includes the minute and a half spent by the female in struggling to get her ventral position after accidentally rolling over upon her back from the position on the right.

The result attained by this performance would seem to be the proper fastening of the eggs to the pleopods, without which the eggs would not develop. During this process the female stays in one corner of the dish and except when turning from one position to another lies so still that it might be taken for dead; only rarely were any of the claws reached near to the abdomen and there is no evidence of any manipulation to secure the attachment of the eggs within the abdominal basket. It is well known that ultimately each egg is firmly tied to the hairs of the pleopods (a few also to some sternal hairs) by a strong string continuous with a tough membrane that envelops the egg as a sort of second shell. These strings and cases are gradually formed, and from some of the cement gland secretions no doubt. For twelve hours or more after the eggs are laid they may be easily pulled away from the pleopods as they are stuck only by a soft glair, but later this glair hardens and force is needed to break the strings away from the pleopod hairs. In one case

when the glair, with many eggs, was taken away from the abdomen soon after laying, new glair was formed within a few minutes. When the egg is freshly laid it is covered by a soft slime that may be squeezed off by rolling it under the cover glass; this material looks like the glandular products above described. The abdominal basket seems full of such material and the eggs sinking down through it are seen in masses on right or left sides according to the position of the female. The pleopods hanging down into this mass are probably pouring out over their hairs more and more of the glandular secretion which will finally harden. By turning the female must let all the eggs fall against now the right and now the left pleopods and again when standing, ventral side down, allow the eggs to dangle down in their coatings of slime till strings would, probably, be pulled out above them attaching each to some part of the pleopod.

As there are four to five hundred eggs laid at one time, in one case 631 eggs by count, it is no light problem to get every one well fastened by its own stalk to the abdominal organs that later serve for their protection and aëration.

Any escape and loss of eggs during the turning action is prevented not only by the abdominal basket of slime with its special apron or surface in contact with the water but by the position assumed by the female; when upon her side the legs under the thorax raise it so that gravity would tend to hold the eggs in the abdominal basket; when upon the ventral side the same is generally true since the abdomen is carried lower and the thorax raised.

After the turning has ceased the glair apron is still in evidence and becoming more conspicuous from discoloration and accumulation of dirt. But after some hours it becomes broken by movements of the pleopods and by straightening of the abdomen and is gradually removed. The claws often have masses of glair upon them and perhaps they assist in removing the superfluous mass. Shreds of glair remain attached to the edges of the tail-fan as late as thirty-six hours after the eggs are laid.

Care of eggs. — Very few eggs fail to become fastened to the pleopods in the above process of turning and henceforth the female bears them so fastened till they hatch. When the eggs

were removed and put into dishes of running water they died, except when taken in very late stages with the embryos well formed. The female takes a certain amount of care of the eggs which seems to greatly increase their chances of hatching; as a rule most of the eggs hatch, but in several cases the eggs upon the abdomen became covered by a fungus which bound them all together into one dead, discolored mass. Still the female bore them till long after they should have hatched. That this fungus attacks the eggs in the open was shown by the fact that one of the 39 females taken "in berry" was found to have moulded eggs when received. The female after laying backs into the darkest, most protected corner available and for a long time keeps the abdomen more or less bent down under the eggs which are then protected from dirt; but at times the abdomen is straightened out and the eggs hanging like bunches of grapes from the pleopods are moved back and forth in a manner well calculated to keep them clean and to insure better aëration, Fig. 7.

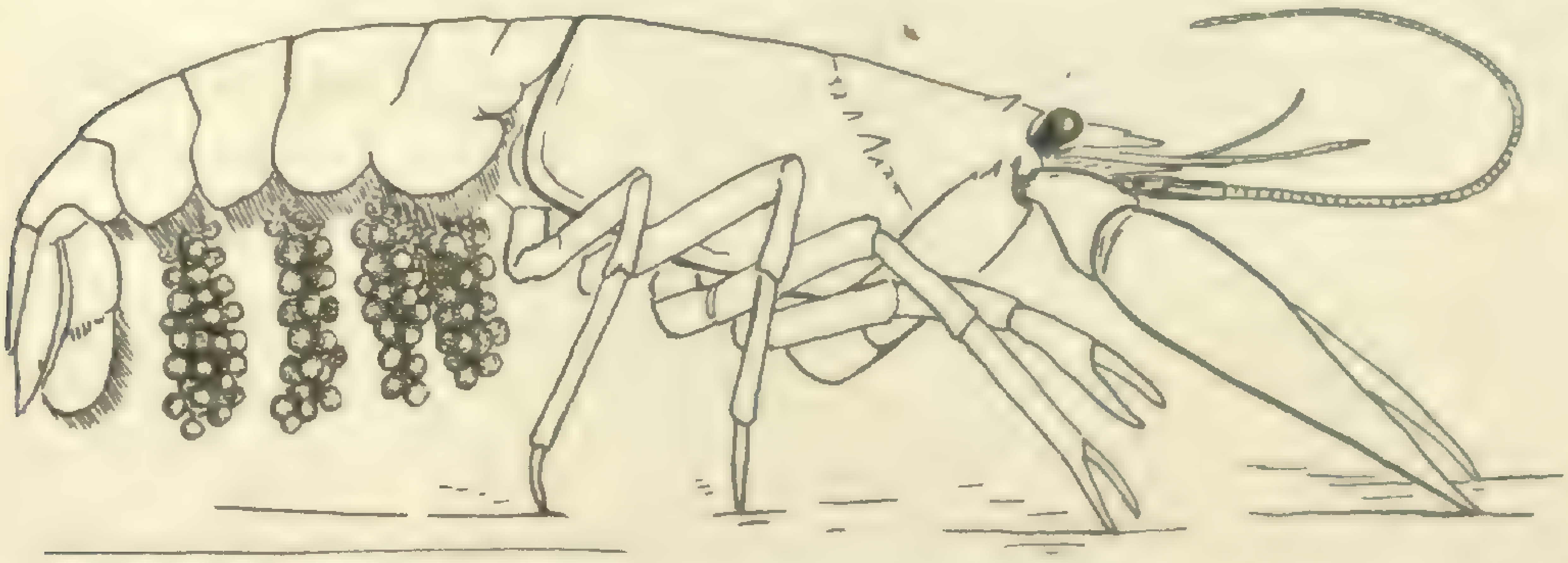

FIG. 7.— Female aërating eggs by raising and straightening abdomen and waving pleopods back and forth. × ⅔.

Sometimes also the female may be seen reaching back among the eggs with her smaller claws as if to examine or to clean them. Some of the females died before the young hatched out and this was more often the case amongst the females that had laid in the open and not in the laboratory. If the eggs were left upon the dead female they became overgrown by mould and died; but if taken a week before hatching and put into a McDonald fish-jar they hatched successfully in considerable numbers.

Fertilization. — As most of the eggs hatch and as sections of freshly laid eggs show sperm nuclei there seems no doubt

that the eggs are fertilized and probably the sperm in the annulus is used for that purpose. But, unfortunately, the mode of fertilization or even its actual occurrence has not been made out. The sperm plug may remain visible for a few days after laying but it then disappears. Its appearance also is changed, its end broken, after laying. Examination of the contents of the annulus after laying showed very few sperms. As the eggs are laid they probably pass over the annulus and a relatively small amount of sperm might fertilize all of them if it came out of the sperm plug at the right time. Before laying the annulus is covered with glair and possibly this may act to bring the sperms out as well as to protect them from the water, which produced marked and apparently destructive changes in the sperms. Some osmotic factor may here be concerned in bringing out the sperm. Other means of getting the sperm out from the waxy tube that we have called the sperm plug and from the interior of the annulus might be: the pressure that the sternal plate between the fifth legs may exert upon the annulus when the legs are forced forward, as sometimes seemed to be the case about the time of laying; or some activity of the small pleopods of the first abdominal somite. The former action, however, seems only to force the annulus to face more vertically in place of horizontally while the necessity of the first pleopods as instruments in fertilization was disproved by cutting them off from a female about to lay and finding that the eggs underwent normal cleavage as if fertilized.

In support of the view that the sperm issue from the annulus at the time of laying it was found that if the annulus was then removed the female seemed not to be inconvenienced, going through turning movements as usual, but the eggs did not develop. This may, however, have been due to the fact that the female was lifted out of the water, the glair disturbed and thus both eggs, and presumably sperm, exposed to the water, which may have prevented fertilization even if the sperm were upon the eggs.

No sperm were found upon the eggs nor upon the annulus: when sperm are taken from the male or from the annulus they undergo changes of form which might make them less

recognizable upon the egg and moreover the egg is 250 times as thick as the sperm and quite opaque.

The whole process of sperm and egg-meeting and union is much in need of elucidation.

Sperm. — While the pairing habits of Cambarus are more complex than those of Astacus the sperm cells are not as complex in form as those described for Astacus by Herrmann. In place of the many radiating arms he figures *C. affinis* has six, as a rule, but sometimes 5, 7 or 8. This is also true of *C. bartoni*. The remarkable bowl shaped vesicle of the crayfish sperm does not have as complex a shape in either of these American forms as it has in Astacus. The diameter of the body is 8 μ while the arms extend out four times that distance on every side so that the entire spread of arms is over 70 μ; but only the refractive vesicle is conspicuous and its longest diameter is less than that of the body.

Period of development, — Attached to the pleopods and presumably fertilized the eggs go through the developmental changes that have been described for Astacus by Reichenbach and others. As these specimens of *C. affinis* were kept in confinement the times of various phenomena could be determined with some precision and in general the eggs of any female develop at about the same rate while the eggs of different females progress differently. Eggs laid near the end of March, 1894, and in 1900, hatched late in May: eggs laid April 11th, 1901, hatched the end of May. In 1903 eggs were laid from March 23d to April 15th; when the eggs were kept in water at 12½° to 14° c some required eight full weeks to hatch; others in a warmer room where the water was not constantly running hatched in six weeks, and some in just five weeks. Most were hatching about May 18th and this was true also of eggs on the females taken April 20th and then in late cleavage or even embryonic stages; so that it seems probable that late in May is a natural time for hatching in the open where these crayfish were taken.

Cleavage. — The nuclear multiplications and migrations of "cleavage" take place but slowly in this heavily yolk laden egg. From sections it seems that the sperm and egg nuclei may

be not far from the surface 12 hours after the eggs are laid, while 24 hours after laying the cleavage nuclei are near the centre of the egg and only about ten in number.

There are only a few cleavage nuclei half way out to the surface 48 hours after laying, while 72 hours shows a large number of nuclei near the surface.

In the live eggs some of the cleavage phenomena may be seen with a pocket lens and are much as described by Herrick for *C. immunis*. At about 72 hours there are rounded areas scattered all over the egg, shimmering through the outer part of the egg; each is about 15 μ in diameter and some 30 of them may be seen upon any face of the egg. When such eggs are crushed under the microscope the dense, clear nuclear areas may be found amongst the yolk spherules and also long bundles of fibres connecting the chromatin bodies.

Eggs taken at earlier times from different females differed and also upon the same female. At about 48 hours a few clear areas might be seen in a group deep within the substance of the egg; some eggs showed 5 or 6, some 30–40, some none at all. Later there were similar areas nearer the surface but upon one side of the egg only. Soon these areas spread so that but part of the surface of the eggs failed to show them and finally they are all over the egg.

After the end of the 3d day the increase of these areas by division is plainly indicated by their shape. From 82 hours on to 7 days there are some hundreds of areas each about 150 to 300 μ, some elliptical, others dumb-bell shaped and others in pairs of rounded areas 150 μ in each diameter. There is now a very striking appearance as of light beads floating above the dark background of the egg yolk. As the areas increase in number they become crowded till they finally touch one another and now in profile stand up as hillocks bounded by valleys and projecting into a space of some 100 μ that is formed between the egg and its case.

In late cleavage the color of the egg, which is olive or yellow green at first but varies much in different females, is now more dark sage green and this color with the clear space about the egg gives the entire mass of eggs upon the female a more

transparent look that enables one to pick out eggs of this period with ease. Under the lens the eggs present a very attractive appearance as the surface has come to be covered by polygonal cell outlines that form a neat mosaic. These cells at first about 200 μ in diameter and containing nuclear areas 100 μ in diameter become reduced to 50 μ.

The eggs are often much flattened spheroids that readily revolve in their cases so as to keep one face upward. The cells flatten down and the eggs again seem smooth.

After this first week there is a period of apparently little change, nearly a second week in which the eggs turn dark brown and at first were thought to be dead. The surface cells no longer show, while the yolk is arranged in large polygonal areas about 150 μ in diameter and not quite in contact with one another. Reagents, however, show the very many small nuclei of the surface overlying these yolk pyramids.

Embryos. — But before the end of this second week the embryo is outlined somewhat as in Reichenbach's Stages A and B; that is in gastrula stages.

In the third week Nauplius stages like Stages F and G of Reichenbach were arrived at in from 18 to 28 days in different batches of eggs. Apparently in connection with the very large amount of yolk in these eggs the embryo is small, only 600 μ on an egg 2000 μ.

About the 30th day the embryo had grown to a length of 1000 μ and was about stage H of Reichenbach, that is with some nine pairs of appendages. However one rapidly developing lot of eggs got to that stage in 21 days and hatched out at the same time as a lot of eggs laid two weeks before this rapid lot. Here a difference of temperature was present and may have caused this unusually rapid development. In these exceptional eggs about two days were spent in passing from stages G to H and nine days from H to J. Reichenbach's final stage K was reached 15 days after J and hatching followed in from one to two days.

In *C. affinis* we thus found that cleavage took up the first week, the beginning of an embryo the second week, to progress as far as the Nauplius the third week and more, to enlarge the

embryo over one half of the egg a fourth week and more and to perfect the embryo for hatching a fifth and sixth week or more. The whole egg development required from five to eight weeks in different sets of eggs under different temperature.

The heart-beat. — When the embryo has grown so large that it occupies half of the shell and the yolk is correspondingly reduced the beating of the heart is quite conspicuous, more than two weeks before the embryo hatches. Its beat is rapid and may be more than one hundred to the minute and there is the remarkable feature of periodic slowing down and even stoppage. In one embryo the heart beat about 150 times in a minute besides resting some ten seconds so that the rate was very great. There were generally five rests in a minute each of one, two or more seconds each and the intervals between rests were taken up with 26 to 36 beats.

Hatching. — The hatching of the eggs as seen in a watch glass with 2-A. took place as follows. The stiff, transparent case within which the embryo has developed splits open along the side next to the embryo's back as a leather ball might if filled with something that expanded. Before this there were seen some muscular movements within the embryo and now the region still containing yolk material was seen to jerk, the antennæ now and then contracted in jerks and the legs moved slightly. The back of the creature became more and more exposed to the water, I Fig. 8. The legs showed seeming spasms of contraction travelling along them and causing local shortenings. The back of the head-thorax and of the abdomen protruded more and more till only the ends of the body and the limbs remained within the shell, II Fig. 8. The larva thus comes into the world back first. In their development the legs and the abdomen have been formed beneath the thorax and bent forward parallel to it, II Fig. 8; but now the legs are straightened out and raised up more nearly at right angles to the thorax and the abdomen also is moved backward and this aids in pushing the larva out to the position shown in II Fig. 8.

These changes have taken some fifteen minutes and after about five minutes more there is a sudden straightening out of the

abdomen which throws the whole creature out into the water as a long straight larva hanging with only the tip of the abdomen left inside the shell, III Fig. 8. The limbs now free in the water kick about and at times the abdomen contracts and since its tip is fast within the shell the result is that the body is brought up near the shell again. The fastening of the abdomen within the shell is brought about by means of a larval skin which is fast to the shell on the one hand and to the

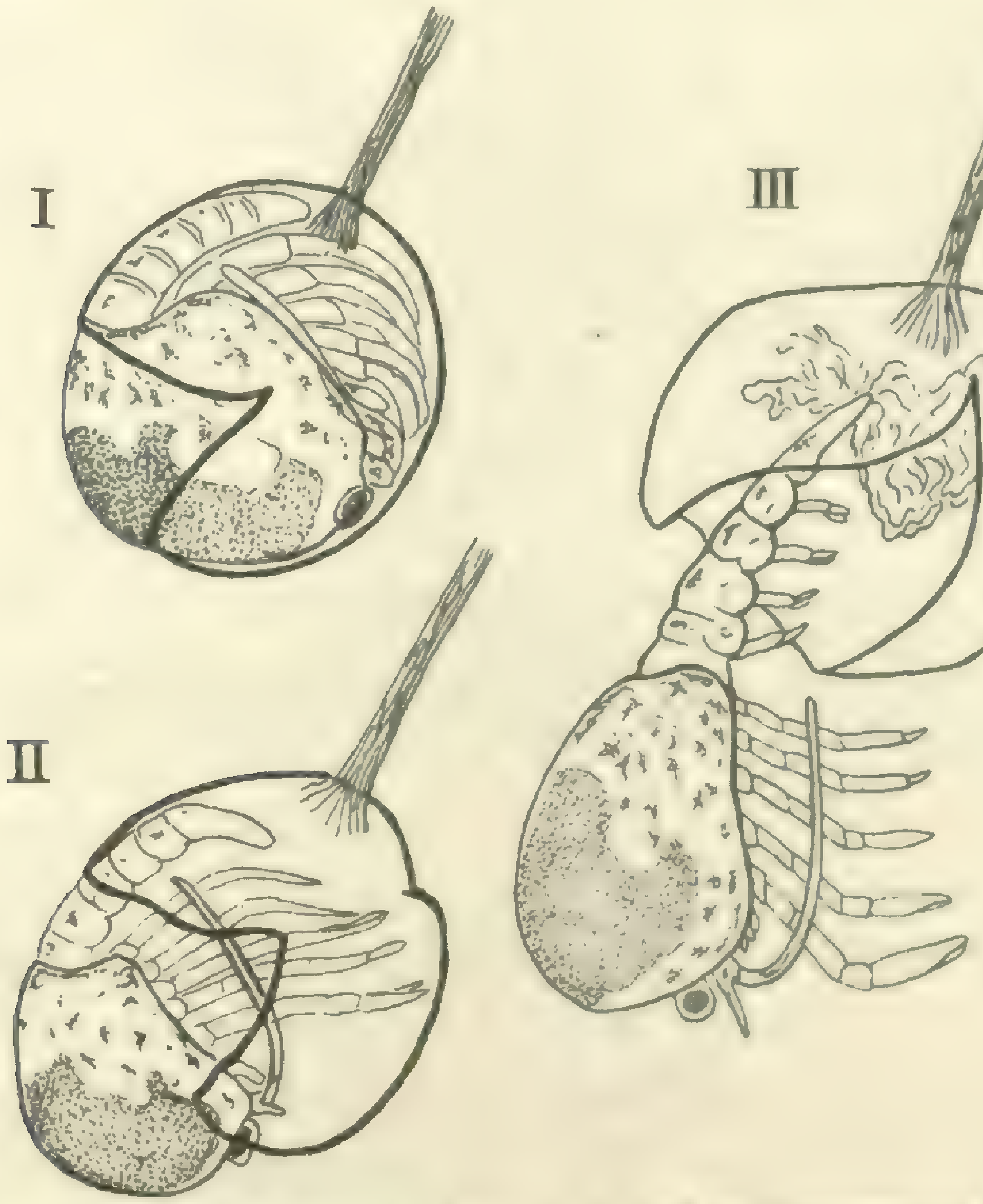

FIG. 8.—Three stages in the hatching of young. In III the larva remains attached by abdomen to cast off skin within egg shell. × 12.

anal region of the larva on the other. This skin was seen at the beginning of hatching as a delicate veil over the eyes and doubtless some of the spasmodic contractions seen along the legs were serving to free the limbs from this embryonic skin. The larva thus moults and hatches at the same time and leaves its cast skin within the egg shell to be made use of as a means of keeping the larva from falling away from the mother, for a time. Hanging thus from the egg the young animal soon begins to spasmodically open and shut its large claws and when the body is brought up to the egg case by the contraction

of the abdomen, now and then, the claws finally clasp hold of the stalk of the egg case. As these big claws have the same larval character found in Astacus, that is recurved or hooked tips, they become firmly fixed in the material of the egg-string and apparently the larva could not get free again. The larva is thus made fast fore and aft, its claws are fast to the egg stalk and its anus is fast to the cast skin within the egg

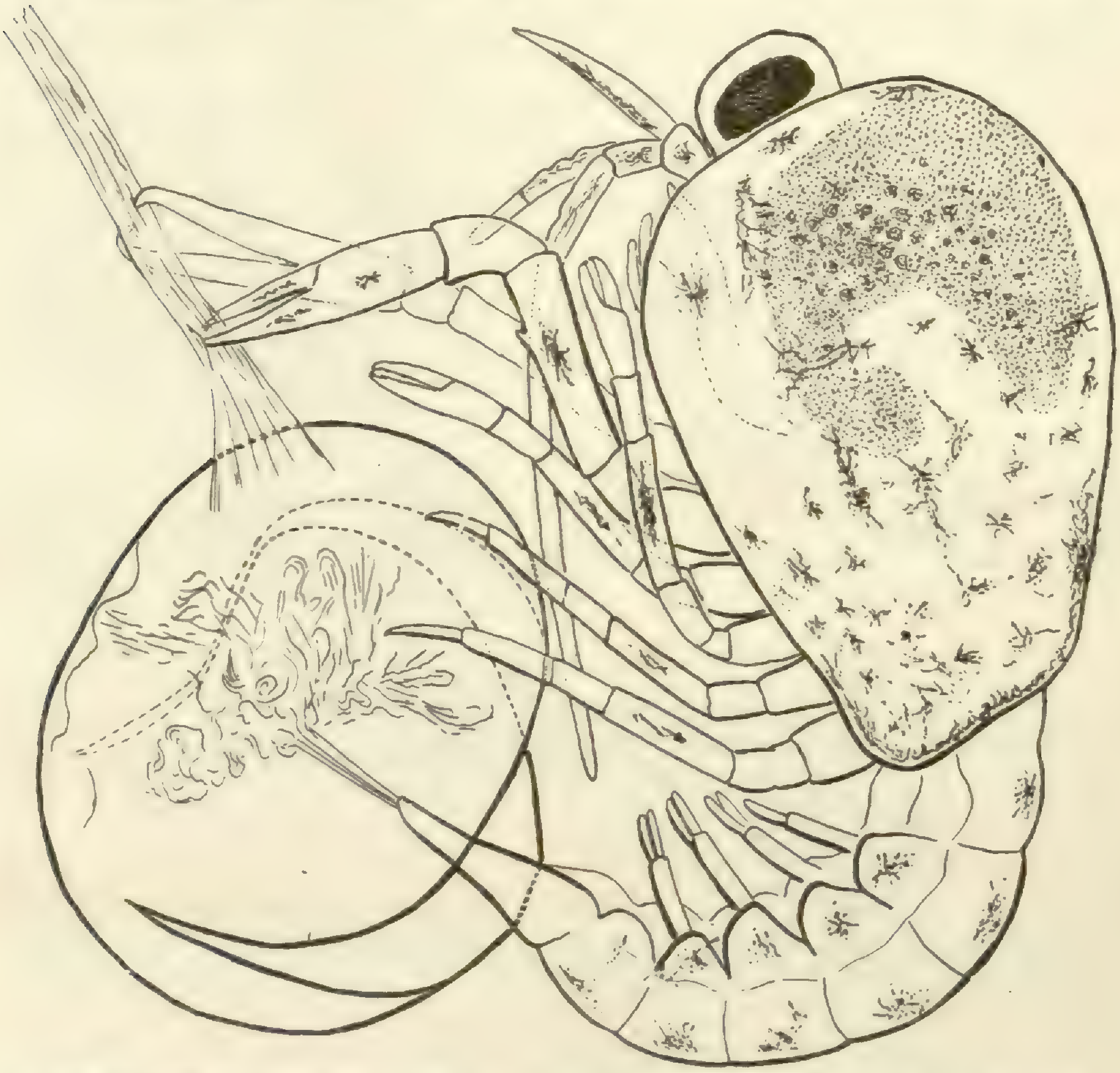

Fig. 9.—Larva 24 hrs. after hatching: claws fastened to stalk of egg shell and abdomen fastened to cast skin inside of egg shell. × 25.

case. As the egg cases are still firmly tied to the pleopods by the strong egg stalks the larvæ live still pendent from and for protection dependent upon the mother.

Such a larva 24 hours after hatching is shown in Fig. 9, As in the European crayfish the young is hatched with a swollen globular head-thorax with proportions strikingly unlike those of the adult, but in life the head thorax is not so dispropor-

tionally swollen as it becomes in preserved specimens. In this region there is still a large, colored, saddle-shaped dorsal area where the yolk material is present.

All the appendages are present as in the adult except the first and last abdominal appendages so that the abdomen terminates with a very simple broad telson and has no wide tail fan. The eyes are very large. The second antennæ which were packed within the egg shell along the edges of the carapace external to the legs, I, II, III, Fig. 8, soon after hatching come to be between the legs right and left, Fig. 9, and in this dejected position add to the general helpless and incomplete appearance of the larva. The rostrum also aids in this infantile expression of the larva as it is very short and blunt and so bent down between the eyes that it cannot be seen except from a ventral view. Both antennæ and rostrum appear useless, or at least to be poorly placed or perfected to be of such uses as they seem to have in the adult.

This larva is so beautifully translucent that the grossly granular blood corpuscles may be seen projected rapidly along the blood spaces in the thorax, abdomen, legs and antennæ. These corpuscles have a long tail-like process behind and by this they often remain fixed till dragged loose into the current again. Scattered over the thorax and abdomen but not upon the telson are large, branching pigment cells of a crimson color and some are found also upon the antennules and antennæ, upon the fourth segments of the legs and upon the big claws as indicated in Fig. 9.

The creature remains fixed but moves its legs and this causes movements amongst the gills which may be seen through the carapace. There are also at times slight jerking movements of the abdominal appendages.

Respiration seems to be carried on very actively, for the very large scaphognathite may be seen through the carapace, as indicated in the above figure, bailing water out of the gill chamber at the rate of perhaps 180 per minute. The establishment of this rhythmic motion so characteristic of many Crustacea is here a slow process. Before hatching the only rhythmic motion seen was the beat of the heart, but after the creature had

emerged into the water this respiratory rhythm was gradually perfected. Two minutes after the larva had first straightened itself out in the water the scaphognathite was seen to swing back and forth but with some stops. Before that at the time of straightening of the body, there were only a few jerky contractions and then, after a minute or more, one or two swings. Five minutes after the body had straightened out in the water the scaphognathite was not in regular swing and even ten minutes was not long enough to acquire an uninterrupted, regular beat.

In some unobserved manner this first or preliminary larva frees its abdomen from the skin within the egg-case, but still remains holding fast by its claws. This larva is about 4 mm. long and lives this life of restricted freedom for only about 48 hours and then moults into a second stage.

Second larval stage.— As the first larva is attached only by its claws we would expect that when it moulted it would become loose and no longer connected with the parent, but such is not the case since it again possesses an anal fastening and later holds by its claws anew. When the moulting takes place the transparent skin of the larva breaks along the back and the back and head of the larva slowly push out through the rent. Then the antennules and antennæ are pulled out of the old skin and for the first time thrust forward into the permanent anterior position instead of being carried backward in the embryonic position retained in the first stage. The legs are pulled out of their old skins and kick about in the water ; then the abdomen is bent free, all but the tip, where the anal region remains fast to that region of the cast skin and does not break loose even when it flaps vigorously. As the shed skin still has its claws fast locked in the egg stalk the larva though it has drawn its hands out of its gloves, as it were, and come out of its old clothes, still remains indirectly fastened to the mother since its telson is fast to its old suit and that is not broken but continuous with the gloves, or claw skins. At first the movements of the legs make the larva seem to be trying to crawl upon the cast skin but after a few minutes the large claws are opened and reaching about take hold of the shed or of the egg case. After many

minutes the claws get fastened to the egg stalk again so that the larva is a second time moored fore and aft; by the claws to the egg stalk and by the telson to the old shed which in turn is also fastened by its empty claw skins to the egg stalk. There are thus two real claws and two empty casts of claws fastened to the egg stalk close together. The new claws are still recurved at the tip but it did not appear that the larvæ were always so firmly fixed that they could not get away or at least be rather easily pulled off during the six days that this stage continues.

This moulting was found to take place also when the first larvæ were removed from the mother and kept 24 hours in running water so that the usual protection of the mother is not absolutely necessary for the future development.

The young in this second stage are about 4½ mm. long and have the form represented in Fig. 10. The head thorax is more elongated and crayfish-like in form. The rostrum though bent down between the eyes is much more prominent and when seen from above it has the characteristic lateral spines. The large eyes are prominently stalked. The antennules and antennæ which have some thirty segments, are carried out in front of the animal and moved about as if of use. The abdomen still ends in a bluntly rounded telson with no sixth pleopods as yet free, but these wide lateral appendages may be seen in bags or cases within the lateral part of the larval telson. The whole body is darkened by very numerous golden red pigment cells which are so crowded at the tips of the big claws that these are conspicuously crimson tipped. The yolk-colored area is reduced in extent and dorsally divided into separate right and left areas posterior to end of which is a large green area. On either side of the stomach a blue area adds to the complexity of the above region. The animal still remains somewhat translucent and blood corpuscles can be seen in places. In the antennæ the corpuscles pass from end to end, a distance of about 2 mm. in a few seconds. The legs bear conspicuous hairs not shown in the figure.

When these second larvæ are taken away from the mother they scramble over one another in heaps and do not walk alone, though if forced apart they can stand upon their legs and walk

Fig. 10.—Second stage of larva: antennæ now extended: attachment of larva to egg-stalks not shown. × 25.

in a feeble manner. Those that hatched in McDonald jars and moulted to the second stage floated about attached to their sheds and to the moulded egg cases. When placed upon narrow strips of cloth they became entangled so that they could be hung up in the water away from sediment and with some such substitute for the maternal pleopods they could be artificially reared, if need be. Larvæ so suspended probably take food for they were seen to pass out long cylindrical greenish fæcal masses 48 hours after moulting. These larvæ were seen to swim only when thrown into Perenyi's liquid when they darted backward with jerks of the abdomen much as do the adults. They live attached to the mother some six days in this second stage and during this time the yolk areas dwindle away to a large extent while the green areas remained and the blue areas stood out as conspicuous organs in the position of the "crabs eyes" on the sides of the stomach.

Third stage.— As seen in a watch glass the moulting of the larva from the second to the third stage takes but a few minutes. The head and thorax break out first, then the legs are pulled out, the abdomen flaps several times and is freed from the old skin entirely. There is now no anal connection of larva and shed and the free telson is found to have the sixth pleopods fully expanded by its sides so that a very wide tail fan is formed and its efficiency as a swimming organ is enhanced by very long plumose hairs. At length the larva has cut loose from its mother's apron strings. Yet it still remains upon the pleopods of its mother crawling about freely over the old sheds and egg cases. When removed from the mother these young walk about upon their long slender legs much like shrimp and when disturbed spring backward with widely expanded tail fan again suggesting shrimp.

These active third larvæ are 8 mm. long from tip of rostrum to end of telson, while the claws stretch out about 2 mm. in advance of the rostrum and the antennæ are 5 mm. long.

The head-thorax is most decidedly elongated and crayfish like. The eyes remain large and conspicuous and add to the shrimp like appearance. The antennæ still have exceedingly large exopodite scales. The rostrum is now straight out in front,

sharply pointed and of the characteristic gothic style of the adult.

The coloring of the larva has been altered by the addition of blue pigment cells over the carapace and legs. The tips of the big claws are no longer crimson but dark red owing to the fineness of the pigment reticulum there. The yolk coloring is gone but the long green hepato-pancreatic areas and the blue "crab's eye" regions show through the carapace.

When these young escape from their connection to the mother they leave behind upon her pleopods the old egg cases and stalks, and the first and second larval skins. These, however, all disappear before very long, but it was not observed whether the female removed them or whether the young may have taken part in tearing them off. The young continue to crawl about upon the pleopods for about a week and before the end of that time the pleopods are cleared of remnants of egg cases.

These free larvæ do not, however, remain continuously upon the mother but gradually make longer and wider excursions into the outer world, returning again and again to the mother. Three hours after moulting some larvæ were found walking about on the bottom of the aquarium and when disturbed they leaped backward several inches with great speed. When the female was lifted up all the young clung fast to the pleopods, but when she was left quiet a few minutes several of the young came off and walk about. The female gave no sign of knowing of the existence of the young but when she walked over a loose larva it turned upon its back, when touched by the pendent mass of young and quickly climbed up amongst the others. But attempts to make the young climb up on to bits of cloth or even shed skins held in a forceps were not successful.

In occasionally swinging the pleopods back and forth the mother was seen to wipe off against the bottom of the tank one of the great number of scrambling young that crowd the pleopods. Such a one at once turned over from its back on to its feet and walked, though it would appear that it probably had had no experience of horizontal surfaces.

The young that walk on the bottom of the aquarium do not

stay away long but return to the mother. Thus two days after moulting some 60 young were shaken loose from a female and scattered upon the floor of the aquarium, but in 20 minutes all but 12 were back again upon the mother's pleopods. Four days after moulting the young crawl all over the mother not only over the dorsal side of the abdomen but over the thorax and the head. As many as a hundred may be off at once walking about in the aquarium and climbing up into the chara plants while a little later only a dozen may be away from the mother. When no screen was used and the water ran strongly the young were carried away now and then and in such manner it may be that city reservoirs, such as those in Baltimore, get stocked with *C. affinis*. Eight days after moulting the young had all left the parents though sometimes a few went back to the maternal pleopods during the next few days. Thus by the fifth of June the young are most all self supporting and independent individuals with no other protection than that they find away from the parent.

How far there is any special recognition between the young and the mother was not determined; but when eight young were taken away from the parent and put in a dish with a female from which the annulus had been removed and which had finally lost all her dead eggs without hatching any they climbed up on to her abdomen and claws but soon got off again. The female did not act as did the real mother but moved about restlessly and wiped her mouth parts as if irritated by the young crawling over them. A few hours later there were no young upon her and four of them had disappeared. Again when several females were kept in the same tank there was some evidence that larvæ sometimes crawled up on to the wrong mother. Moreover in 1900 it was noticed that when a dead female was lifted from the water the young that dropped off returned again to crawl upon the dead crayfish and remained even when the parent was far advanced in decay. When the abdomen was broken open the young crawled upon the exposed muscles for a time but later were upon all parts of the abdomen except the broken surfaces.

Later stages.— By keeping the young of a single mother in a

tank by themselves some facts were made out as to the subsequent moultings during the rest of May, June and the first half of July. These young had a large aquarium with good supply of mud, Chara, anodons and various plants and insects with running water, sunshine and shallow water for good aëration. The young remained in the third stage for about 18 days and their color gradually changed from red to greenish owing to the great increase in the blue pigment. The legs also developed bands of dark color across them though otherwise almost invisible, yet the big claws stood out as reddish objects with blue at the base. The fourth stage had about the same coloring but being so much larger it was much more easily seen. The rostrum-telson length was 12 mm.: the claws reached out 2 mm. in advance of the rostrum: the antennæ were about 8 mm. long: the thorax was 2½ mm. wide, and the tail-fan expanded 5½ mm. One of these larvæ had short, simple papillæ upon the first abdominal segment to represent the pleopods, apparently of the female. These young were still translucent enough to show the beat of the heart, at a rate of about three beats to the second, and the circulation of blood corpuscles in the antennæ and legs, though the muscles were now much more conspicuous. The effect of the red pigment cells was everywhere toned down by the widely diffused blue cells.

In about 17 days, that is July 1st, many of the young had passed into a fifth stage. The length was now 15 to 18 mm., with the thorax about 3 mm. wide and the tail-fan 8 mm. The color of this fifth stage was white on the ventral side and elsewhere this was overcast by greenish. The legs were now white with dim transverse bands of gray while the large claws had lost the red and showed brilliant blue at the base of both finger and thumb.

The young move about actively, in walking they move the fore pairs of pleopods back and forth very rapidly. They swim readily and are still shrimp like in movement and in appearance, as they have long slender legs, protuberant eyes and wide tail-fans.

Within a week some larvæ were found in a sixth stage with a length of 21 mm., a thorax width of 5 mm., a tail-fan expanse of 11 mm. and antennæ about 19 mm. long.

Some eleven days later a very large larva was found with a length of 29 mm., a width of thorax of 7 mm., claws projecting 8 mm. beyond the rostrum, antennæ 25 mm. long and a tail-fan expanse of 14 mm. This creature was then a crawling crayfish with less tendency to keep high up amongst the water plants: it also was dark greenish, finely speckled, and there was blue on the legs. Little translucency was left and the animal looked much like a diminutive adult. The large claws were still marked with blue and had dark red at their tips.

This specimen was a male with two long, scroll-like pleopods carried forward in the groove under the thorax as in the adult and the following four pairs of pleopods were not modified: thus the male now has but one pair of modified pleopods as is the case in the lobster.

We may summarize the growth and moultings of the young of a single female during two months as follows. The eggs laid the night of March 28th, hatched into a first stage May 18th. With a length of 4 mm. they lived two days and moulted into a second stage. This second stage was 4½ mm., long and lived six days from May 20th. The third stage was 8 mm. long and from May 26th lived 18 days. The fourth stage was 12 mm. long and from June 13th lasted 17 days. The 5th stage was 15–18 mm. long and lived from July 1st five days. The sixth stage was 21 mm. long and from July 6th, lived eleven days. The seventh stage was 29 mm. long, and from July 17th lived an undetermined time as observations were then discontinued. The first and second stages remained attached to the mother for about one week and were not more than 4½ mm. long. The third stage, 8 mm. long, kept on or near the mother for about a week and then lived an independent existence for a week. The following stages were all independent and gradually took on all the adult proportions and colorings.

Growth of young crayfish. — The young were left in a tank with running water, mud, water plants, anodons and frequent feedings with raw hen's egg till October 6th. Then only eight survivors from a hundred or so were found. These were then measured and as seen in Table I they varied greatly in the amounts they had grown, though all were hatched from the eggs of the same mother.

Table I. Measurements of eight brothers and sisters 141 days after hatching.

TABLE I.

	1	2	3	4	5	6	7	8
Length: telson rostrum . . .	62	55	53	49	50	45	43	41
" " chela	75	75	62	65	60	55	41 ?	47
" antenna	37	51	48	46	34	43	—	25
Width: thorax	15	15	14	13	12	11	11	10
" tail-fan	25	23	24	22	25	20	20	19
Sex	♀	♂	♂	♂	♀	♂	♂	♀
Length: anterior male organs .		9	9	9		8	7	
" posterior " " .		10	10	10		9	7	

Ten other young from various females hatched about the same date as the above and measured October 7th gave the following results, Table II.

TABLE II.

	1	2	3	4	5	6	7	8	9	10
Length: telson rostrum	60	59	52	52	45	39	40	33	30	22
" chela-telson	74	65	65	68	55	50	50	41	35	27
" antennæ	45	30	47	46	25+	—	22+	—	20	16
Width: thorax	14	14	13	12	11	10	10	8	8	6
" tail-fan	26	25	23	24	20	20	19	16	15	10
Sex	♂	♀	♂	♂	♂	♂	♂	♂	♂	♀
Length: first male organs . . .	10		9	9	7	6	6	5	4	
" second male organs . .	11		10	10	8	7	7	5	4	

Taking the two tables together the largest crayfish was 62 mm. and the smallest 22 mm. long; the average length was 46 mm. During these two months and three weeks of summer some few seem not to have grown at all, while about one third of them have almost doubled their length. The great difference between the largest and smallest is but imperfectly represented by the above figures: thus the specimens, 10 of II and 1 of I, being in length as 31 to 11 seemed in bulk much more widely apart and in weight they were found to be as 13 to 7. Only 5 of the 18 were females but it is not known when this preponder-

ance of males arose, whether before or after hatching. The males have now two pairs of very conspicuous and well formed sexual pleopods of great size; the exterior pair are a little less and the posterior pair a little more than $\frac{1}{6}$ the length of the crayfish, but this ratio is the same in the adult. In these young males the antennæ often look longer and more tapering than in the females and that this may now be a secondary sexual character would seem to follow from the measurements. The eight males with perfect antennæ averaged 50.75 mm. in length and their antennæ were 42.875 mm., or 84% of the length of the body. The five females averaged 47 mm. in length and their antennæ 31.4 mm., or hardly 67% of the length of the body.

Under such conditions the young of *C. affinis* may then attain a length of two inches in their first summer. Additional data for knowing their rate of growth were obtained from some young hatched about June 1st, 1901, from eggs laid April 11. These young were kept in a large sink with running water, mud, water plants and anodons which dying from time to time probably gave them food material. The twenty survivors were measured February 11th, 1902, or 8½ months after hatching and the lengths and widths as well as the sex are given in Table III. The sexes could be readily determined as the females had conspicuous annuli and the males well developed sexual pleopods.

Table III.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Length	41	38	24	56	32	44	43	39	39	33	35	36	32	34	30	23	30	29	27	32
Width	10	9	6	14	7	11	10	10	9	8	8	9	7½	8	7	5½	7	7	6	7½
Sex	—	♂	♂	♀	♀	♂	♀	♀	♂	♀	♀	♀	♂	♂	♂	♀	♂	♀	♂	♂

Number 4 may have been introduced by mistake: the others range in length from 44 to 23 mm. with an average of 34 mm. None are as long as two inches: one half are about 33 mm. and 80% above 29 mm. The sexes were about equally distributed, 10 males and 9 females.

These young did not attain to as large a size as those in the

preceding tables though they were four months older. But this additional time was autumn and winter and it would seem probable that the crayfish of Table III not being as well fed as the others had not grown quite as fast during the summer and had then remained stationary. Though they were kept in a warm room they were in running cold water.

The above twenty crayfish of table III were then kept in the same conditions during the rest of the Winter, Spring, Summer and Autumn and until December 5, 1903. The only two survivors were both females and at that time, being 18 months old, gave the following measurements. One was 70 mm. long and 16 mm. wide: the other 79 mm. long and 20 mm. wide. Since last measured, a space of ten months including a summer, each had *probably* doubled its length.

These two were left in the same surroundings, except when removed for breeding as below described, and measured again July 1st, 1903, when 25 months old. One was 79 mm. long and 20 wide, and the other 76 mm. long and 20 wide. The latter was clean and bright and the former dark and dirty as in winter so that we infer the smaller one had recently moulted and added 6 mm. or about $\frac{1}{12}$ to its length and $\frac{1}{4}$ to its width.

During their third summer these two females were kept with the young of Table I and thus had better food conditions. Only one survived till October 6th and then had a length of 90 mm. and a width of 24 mm., while its tail-fan expanded 43 mm. It had thus gained more than 10 and perhaps as much as 14 mm. in length or added $\frac{1}{8}$ to nearly $\frac{1}{5}$ to its length.

Summarizing the above data we see that the young of *C. affinis* reared in the above conditions of captivity hatch in May from eggs 2 mm. in diameter as larvæ 4 mm. long and there pass through stages of 4½, 8, 12, 15–18, 21 and 29 mm. during the first two months. During the next three summer months they increase to an average length of 40 mm. but may grow as long as 62 mm. During their first winter they may, probably, not grow at all; but in the second summer they may reach a length of 70–80 mm. In the third summer the length may become 90 mm. as indicated by the sole survivor at 28 months.

That this crayfish grows in the open about at the rate above indicated seems not improbable from the measurements made upon 80 specimens of *C. affinis* taken early in October, 1903, from a small pond in Baltimore that had been stocked a few years before. Five of these were 85–100 mm. in length and obviously belonged to a different period of life as there were none between these and 65 mm. lengths. The remaining 75 ranged from 65 to 32 mm. There were only 6 below 40 and 12 above 56; the remaining 57 were from 40 to 56 mm. long. Thus 76% were from 40 to 56 mm. long and we may believe these were hatched that same Spring and were about 4 months old; the same would apply to the few smaller ones. The 12, or 16%, that were above 56 and not above 65 mm. long are too small for young that had passed a second summer and probably were of the same age as the majority. The five largest specimens were too large for second summer crayfish and probably were at the end of their third summer. The absence of any in what we would regard as second year lengths may be perhaps connected with the draining and drying that the pond suffered some winters.

Sexual maturity.— In rearing crayfish it was found that their sexual instincts and organs mature long before the maximum size was attained. Some of the young represented in Tables I and II were found to unite in pairs in October when but 4½ months, or 141 days old. These very small crayfish, two inches long, thus had their sexual instincts developed. Moreover the sperm taken from the male is then, apparently, just like that of the full grown males. The females 1 and 5 of the first table had sperm plugs, though the other females did not. These females were 62 and 50 mm. long. The female No. 2 of the second table was clasped by male No. 3 and subsequently had a sperm plug: this female was 52 mm. long. Whether these females of 50, 52 and 62 mm. in length will lay eggs next spring remains to be seen. The males seen to unite with females were 55 and 59 mm. long.

The two females described in the last section when 70 and 79 mm. long and 22 months old were put with males April 10, 1903. Though they had been alone for some months they at once were united with the males and the annulus of each

showed a sperm plug as it did not before. When they were 23 months old they both laid eggs.

Amongst the females that laid eggs in captivity there were both long specimens 120 mm. long and smaller ones down to even 75 mm. From their size we infer these small ones were about to begin their third summer. Thus though the sexual unions take place at the end of the first summer we have, as yet, no evidence of eggs being laid till the beginning of the third summer. However the autumnal union in the first year was found not only in the specimens reared in confinement but among those eighty above mentioned as taken in the open. And here it occurred both in the laboratory and in the pond and not only between the larger, third year sizes but between those of 56 mm. which, probably, were in their first year.

We see then that little specimens of *C. affinis* may have mature sexual instincts and unite in pairs in the autumn when they are but 4 months old and 50–60 mm. long, but as yet it is not known if they lay before they are 23 months old and 75 mm. long.

Finally.— In connection with the development of sexual maturity we may here refer again to the apparent sexual difference in lengths of antennæ noticed in connection with tables I and II. When the above 80 crayfish taken in the Autumn and thought to be most all of the first year, like those of the tables, were measured little difference between the lengths of the male and female antennæ was found. Throwing out the specimens with broken antennæ there were 37 males with an average length of antenna of 42 mm. and 36 females with an average length of antenna of 41 mm. Again the average male antenna was 81.3% the average length of the male body while the same for the female was 78.9%. The differences are so slight that, considering the errors in measurement, there seems here not enough evidence that the females have the shorter antennæ as a class.

BALTIMORE, November 5, 1903.

NATURAL HISTORY OF HAMINEA SOLITARIA SAY.

W. M. SMALLWOOD.

THE shell-bearing species of the family Bullidæ have been found freely distributed in the rocks since the Tertiary period. A large number of species have been found as fossils. Ludwig in Leunis *Synopsis der Thierkunde* states that there are between two and three hundred recent species. They have a wide distribution in both European and American waters, being commonly found in the sandy and muddy bays of the temperate regions.

The Bullidæ belong to the general order of Opisthobranchia and to the suborder Tectibranchia.

Thomas Say read before the Academy of Natural Sciences at Philadelphia on July 24th, 1821, a paper in which he gives "An account of some of the marine shells of the United States." In this article we have the first reference to *Bulla solitaria*. His description is as follows: "Bulla solitaria. Shell remarkably thin and fragile, pellucid, oval, narrowed at base, with numerous impressed, revolving lines, and transverse very obtuse wrinkles; apertures surpassing the tip of the shell; spire none, substituted by an umbilicus; umbilicus of the base none, less than half an inch. Inhabits the southern coast of the United States.

July 4th, 1835, J. G. Totten described a species of Bulla, variety *insculpta* which he dredged in about fifteen feet of water from the muddy bottom of the harbor at Newport, R. I. He maintains that *insculpta* is distinct from *solitaria* because of some slight variations in the color and shape of the shell. He says, "Thus (insculpta) can hardly be Say's Bulla solitaria. It is not umbilicated at the top as that species is; having merely a shallow pit in which nothing of the interior whirls can be seen. The solitaria is described as being narrowed at the base; but though our shell is regularly rounded in the passage, below, of

the right into the left margin, it is widely rounded; and the widest part of the shell is below the middle."

A. A. Gould, in his *Invertebrata of Massachusetts* ('41), considers *Bulla insculpta* and *Bulla solitaria* identical: he concludes his description of *Bulla insculpta* with the following paragraph: — "The differences between solitaria and insculpta, if there be any, must be very slight. Nor do I see that the two descriptions (Totten and Say) are at all inconsistent with each other. Still it is true that the shells from Martha's Vineyard are precisely like those from Charleston, S. C., and accord with Mr. Say's solitaria; and those from Roxbury are precisely like those found by Col. Totten at Newport, R. I., and described by him. The observable differences are, that the first are of a more dead white, are more cylindrical, the summit has a more square appearance, the revolving lines are less distinct, and there is always a perceptible opening in the region of the spire. These differences may be ascribed to age or locality."

Verrill ('73) describes *solitaria* as occurring along the Atlantic coast from Massachusetts Bay to South Carolina and makes no mention of *insculpta* except to assume that it is the same species as *solitaria*. The shells of *insculpta* and *solitaria* as figured by Totten, Gould, and Verrill seem to be identical.

The size of the shells which I have found at Wood's Holl, Mass., varies to a considerable degree; one shell found was only one-fourth as large as the average, the shape of a large number of shells which were examined varies in regard to the width and length of the lip. All of the shells examined were dextral. The distinctness of the revolving lines seems to depend on the age, the larger ones being the more distinctly marked. The statement that the shells of *insculpta* seem to be more of a dead white color than that of *solitaria* is easily explained. The shell of the living animal is a golden gray; the golden tinge being given by the thin structureless membrane, the periostracum, which completely covers the shell (Fig. 1). When this membrane has suffered disinte-

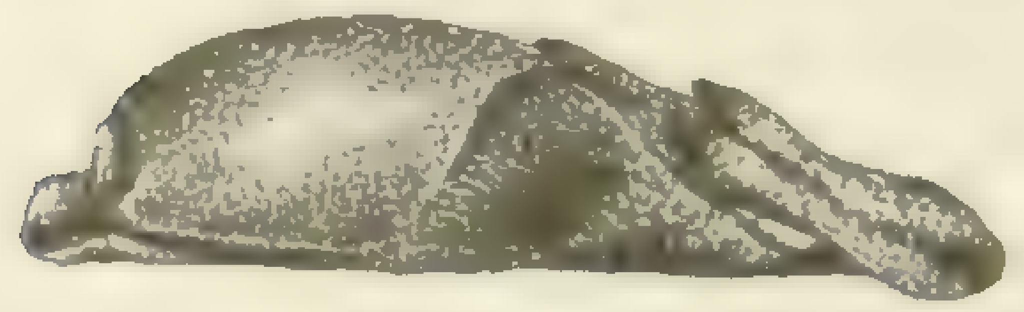

FIG. 1.—*Haminea solitaria* showing the proboscidial snout and tentacular disks. The parapodial folds conceal the anterior part of the shell and the mantle extends posterior to it. Natural size.

gration the shell has the dead white color mentioned by Gould. In view of these variations I think that the shell as originally described by Say is identical with the *insculpta* of Totten and is the *solitaria* found in the vicinity of Woods Holl, Mass., and of Long Island, N. Y.

Pilsbry has decided to limit the family Bullidæ to the single genus Bulla. Formerly the members of the Akeridæ were included with the Bullidæ but the character of the radula, form of the shell, and relation of the animal to it enables one to sharply differentiate the two families.

The Bullidæ have in the radula a few longitudinal rows of teeth (formula I. 2. I. 2. I.). The animal is capable of complete retraction into the shell. There are no epipodal or parapodal lobes; the foot is long and tapering behind. The shell has a mottled color pattern.

The animal described by Say, Totten and others and referred to in this article is placed by Pilsbry[1] in the family Akeridæ and in the genus Haminea. "The Akeridæ are a much lower stock of Tectibranchs than Bullidæ, retaining the primitive multi-dentate radula, and the epipodal lobes, and having a thin, fragile unicolored shell.

The following is the specific description of *Haminea solitaria*: "Shell thin, subcylindrical, with gently convex sides, truncate vertex and rounded base; color horny or light brown. Surface shining, having irregular growth wrinkles and (under a lens) *fine, deeply impressed spiral grooves*, much narrower than their intervals, sometimes with smaller ones intercalated. Vertex white, somewhat impressed in the middle, subperforate. Lip arising to the right of the center, slightly thickened; outer lip gently arched forward. Columella thin, concave. Alt. 10, diam. 6½ mill" (Fig. 2).

FIG. 2.—The shell of *H. solitaria*. × 2.

Habitat.—Until the report of Verrill, ('71–'72) nothing was said of the animal or its natural history. All writers confined themselves to a conchological description of the species. Verrill says that *solitaria*

[1] *Manual of Conchology.*

"is restricted to muddy shores and bottoms, in sheltered situations and is found also in muddy ponds and estuaries." Smith and Prime state that the animal is rare, found in mud at a depth of one or two fathoms. Balch ('99) states that the animal, "Haminea solitaria, Bulla solitaria, is rather uncommon alive, sometimes occurs on marsh grass, top of sea walls." In regard to the general distribution of this species Verrill says, "From Mass. Bay to South Carolina it is common in muddy lagoons and salt ponds, in shallow water where not too brackish, along the shores of Vineyard Sound, Buzzard's Bay, and Long Island Sound. Abundant in a small pond near Holme's Hole, in New Haven Harbor, in ditches near Fort Hale."

Haminea solitaria is found rather commonly in the Eel Pond and Big Harbor at Wood's Holl, at Hadley Harbor, and at the bathing beach on Buzzard's Bay at Wood's Holl. During the laying season the animal migrates into shallow water and may occasionally be seen upon the eel grass and algæ, but usually not in water less than two feet deep at low tide. If the eel grass be disturbed they drop at once into the water and fall to the bottom, where it is very difficult to see them, owing to their form and color being so similar to the ordinary weeds and mud at the bottom; thus it is practically impossible to gather animals by looking for them on the weeds or bottom. They have been secured in two ways: first, by taking an ordinary fine-mesh dip net and skimming off the sea weeds and half an inch of mud from the bottom, then carefully washing out the mud; in this way a number have been secured in the shallow ponds and lagoons about Wood's Holl; secondly, by dredging; this method is necessary in deep water. Bulla may be found, even in the breeding season, in water thirty feet deep in the Big Harbor at Wood's Holl, — the greatest depth where they have been found. This peculiarity may be due to the fact that their former laying spot in shallow water is now occupied by a deep sea wall. Dr. Charles B. Wilson obtained a number of *solitaria* by skimming in clear water near Edgartown about the 18th of August. He was sure that the net did not pass over any eel grass or sink beneath the surface. I feel sure that this is the real explanation of the occurrence of Bulla in great abundance

just before the egg-laying time, and their equally sudden disappearance after the egg-laying time. They simply rise to the surface and swim away.

In the summers of 1897 and 1898 most of the specimens obtained by me were collected in the larger of the two so-called "oyster ponds" near the Marine Biological Laboratory. Although a large number of capsules were taken from this place, over one hundred capsules were gathered from another locality and put into this lagoon in order to assure an abundance of material in succeeding seasons. In the summer of 1899 no capsules could be found in this lagoon, in the summer of 1900 three capsules were found here, but all of the eggs had died before reaching the twenty-cell stage ; the tide flows freely into the lagoon thus keeping the water comparatively fresh. The drainage from the Marine Biological Laboratory flows into an adjacent lagoon and it is possible that the water seeping through may have some poisonous effect which kills the eggs and has destroyed or driven out the animals themselves.

The Bulla found on the sandy bathing beach at Buzzard's Bay occurs about half an inch below the surface of the sand ; usually near the capsule, which is the only indication of the presence of the animal.

General Morphology.[1] — It is not my purpose in this section to go into the details of the various systems of organs except in so far as they are directly related to the development of the egg ; I purpose, however, to give a brief sketch of the general form of the animal.

Probably the most striking feature of this species is its color, which is a golden gray thickly mottled with dark brown and occasional orange spots ; one might almost say that the gray background looks as though sprinkled with fine sand. The shell is translucent and slightly striated spirally ; it is not at all glossy or shiny. One would hardly expect to find much of a shell in a tectibranch, but in *solitaria* the reduction of the shell

[1] For a full discussion of the Morphology of the family Haminea (Bullacea) see M. Vayssiere, Recherches Anatomique sur Les Mollusques de La Familles des Bullides *Ann. Sci. Nat.* Tome 9. 1879. R. Bergh. Bullacea. *Reisen in Archipel d. Philippinen*, pp. 211–312, 1901.

has only just begun. The most noticeable feature in this process is the fact that the shell is thin and fragile, so much so that it must be handled very carefully. The second feature is that in the mature animal the shell is not large enough to shelter the whole body in its contracted state. The shell certainly cannot afford particular protection against enemies, but when we remember where the animal lives and its habit of crawling along the mud and sand, we can readily see that it could have no better protection than its color. It imitates the color of the roots of eel grass most closely; at first sight I have often mistaken the detached fragments of these roots for Haminea.

The size of the animal depends largely upon age; the smallest shell measured was three mm. in width, and five mm. in length; the average size of the mature shell is 7 mm. in width, and 10 mm. in length. The average length of the extended animal including the shell is 2 cm.; the smallest animal was 8 mm. in length. I can make no definite statement as to the age or size at which *H. solitaria* begins to lay, but can say that I have never known the smaller ones to lay. In the aquaria the animals die after laying, but I do not believe that this fact can be used as proof that they always do.

The foot of Haminea possesses, though not clearly distinguished, the three divisions characteristic of the typical molluscan foot. From the mesopodium arise the parapodia; these are lateral lobes, or folds, like extrusions of the edges of the foot. In some of the Opisthobranchia the parapodia (epipodia of Pilsbry) are highly developed and unite upon the back, completely covering the shell. In our species however the parapodia cover only the anterior part of the shell.

The young animal moves by stretching forward the head and foot, and then drawing the visceral mass forward, so that the progress results from an alternate stretching and contraction of the anterior flexible part of the body. The posterior part being drawn ahead at each contraction. In the mature animals there is no such noticeable division in the movement; with them locomotion is apparently a continuous gliding process.

The anterior part of the animal terminates in a broad thin proboscidial snout. Running back from the end of the snout

there are two tentacular disks, which are divided only part way. There is very little movement in these disks, except as they shift about over the anterior portion of the shell. In this species there seem to be no special sense organs in the tentacular disks. So far, I have been unable to explain their function. The tactile sense is usually located in the tentacles, but in our animal the anterior portion of the snout performs this function, as is very evident from its movements. In many of the Opisthobranchia the mantle folds over part of the shell, but in *H. solitaria* the only external evidence of the mantle is a thick fold which occupies the lip of the shell and extends back of it for about four mm., it is here extended and affords a surface equal in width to the shell. At first sight one would think because of this arrangement that the foot extended from the snout to the posterior portion of the animal, but closer inspection shows a sharp demarcation which indicates the boundary between the posterior portion of the meso-podium and the mantle. All of the parts of the body that are exposed are covered with columnar, ciliated epithelium. A great quantity of mucus is secreted by the animal, so that in crawling about the dish they often leave a nearly perfect tube of mucus. This is secreted by numerous typical single-celled glands, which are especially abundant at the edges and tip of the snout, and the outer portion of the tentacular disks.

The especial characters aside from the shell which distinguish *H. solitaria* are the stomach plates and the form of the radula.

FIG. 3. — Showing the arrangement of the stomach plates, each of which is imbedded in a large amount of muscle. The free surfaces are so arranged as to triturate perfectly the food.

There are three stomach plates so arranged that the food is trituated by them (Fig. 3). The plates are composed of chitin, having their bases firmly imbeded in the strong muscles of the stomach. The form of a single plate is shown by the camera drawings (Figs. 4, 5). The portion of the plate that comes in contact with the food is differentiated into a number of ridges which are larger and more pronounced at the anterior end. The

largest teeth are found on the anterior part of the plate, having a triangular form. The size and prominence of the teeth gradually decreases toward the posterior part of the plate. This gradual increase in size of the teeth and the ridges indicates how both are continually forming to take the place of the more anterior ones as they become worn out. The youngest teeth are those found on the smallest ridges. In some instances it is difficult to be certain that teeth are even present.

FIG. 4.—One of the chitinous stomach plates as seen from the free surface. × 24.

FIG. 5.—One of the chitinous stomach plates as it appears from a profile view. × 24.

The radula is an interesting structure but one that is difficult to represent in a drawing. When this organ is removed from the animal, it is somewhat triangular in shape (Fig. 6). In the center of the anterior part there is a single row of teeth, having a broad free margin and terminating at each side in a rather broad blunt process (Fig. 7). There are an indefinite number of long, slender, sharp teeth arranged in rows which correspond to the teeth of the median ridge. The bases of these lateral teeth are imbeded in the muscles of the radula (Fig. 8). Each lateral tooth is bent at an angle of about 90 degrees. This arrangement of the teeth would give the following formula for *H. solitaria* ∞. I ∞.

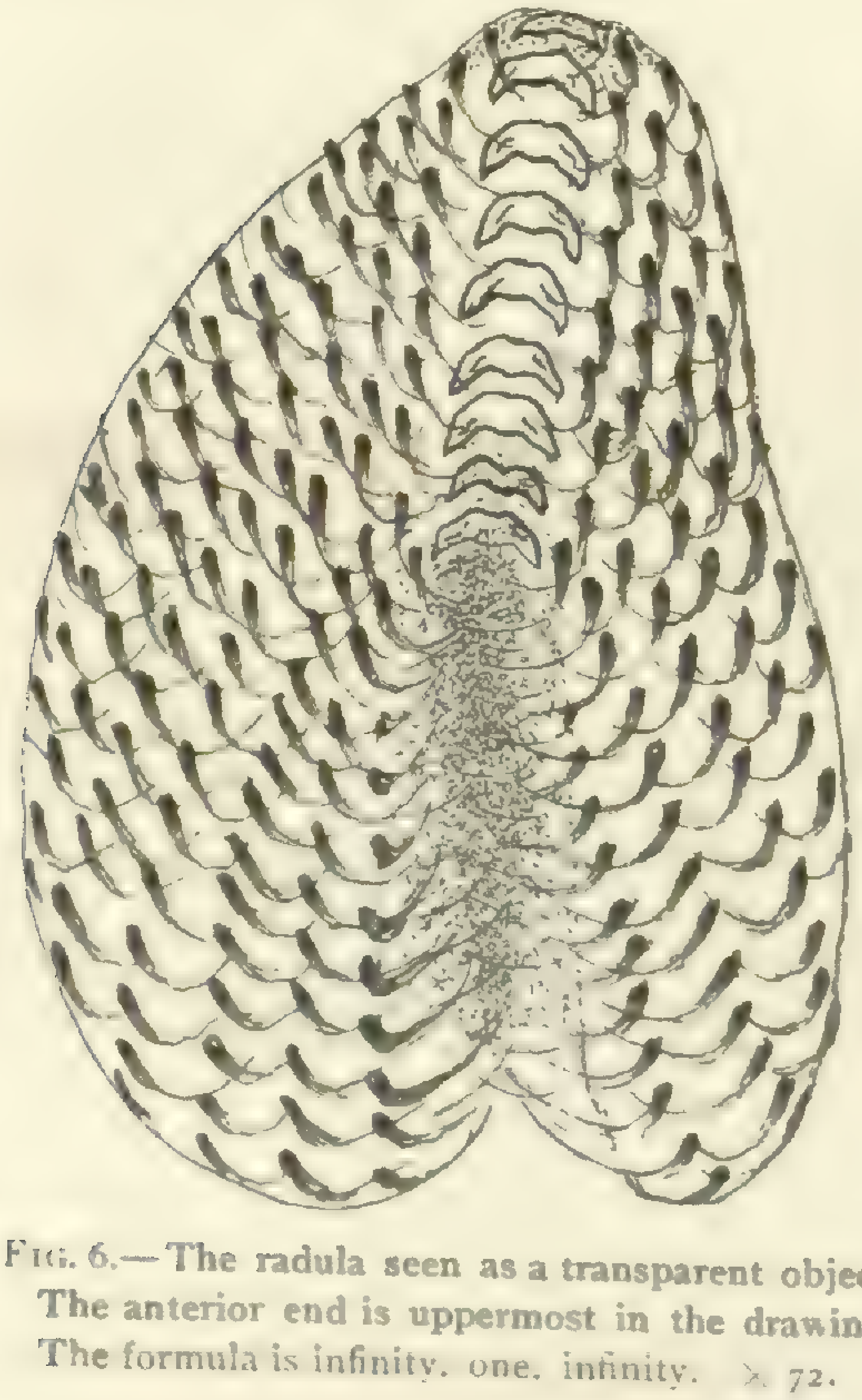

FIG. 6.—The radula seen as a transparent object. The anterior end is uppermost in the drawing. The formula is infinity. one. infinity. × 72.

The genital organs.— This system of organs is fully discussed by Lang; I have been able to demonstrate of all the

parts as given by him and will, therefore, quote freely from his description. The Opisthobranchia are all hermaphrodites. Haminea is no exception to the general rule and comes under the first type as described by Lang. The germinal gland consists of numerous "converging diverticula." The eggs and spermatozoa arise from the same part of the gland and are intermingled. During their development they become detached and lie free in the cavity of the gland. The ducts of *H. solitaria* are considerably complicated, because of the development of the accessory organs. The ovotestis lies between the lobes of the liver and the posterior part of the body; this gland has numerous branches, which finally collect into the common hermaphroditic duct; the duct empties into the common genital cloaca. The genital aperture opens into the extreme right anterior part of the mantle cavity, and from it there is, continued forward, an open ciliated furrow, which carries the spermatozoa to a gland called the "prostate"; this opens into the penis. "The penis itself lies in the right, on the boundary between the head and foot. When it is at rest its sheath lies in the cephalic cavity near the buccal mass." Two important glands open into the genital cloaca by a common duct; first, the albumen gland, which is comparatively small and lies upon the surface of a second, known as the nidamental gland; the latter is much larger than the former and yields the outer protective envelope of the egg. The albumen gland supplies the albumen for the egg capsule.

FIG. 7.—Three of the median plates from the radula. × 390.

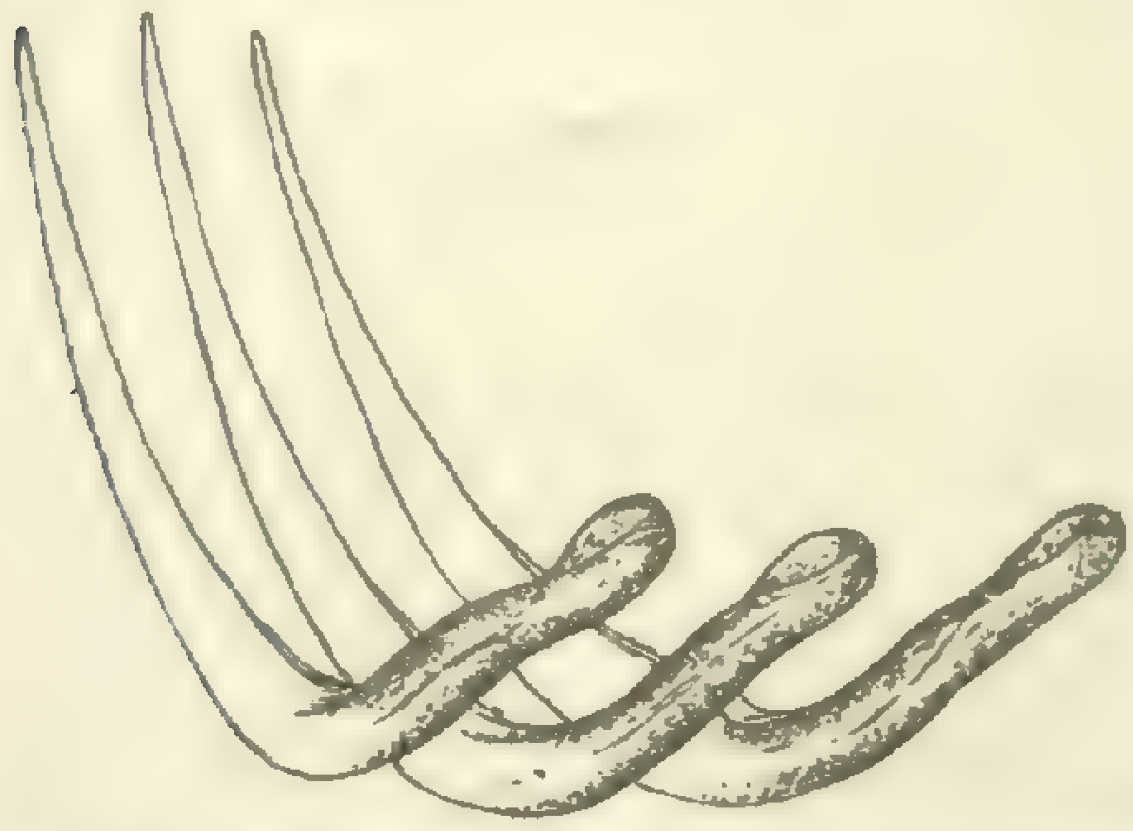

FIG. 8.—Three of the lateral teeth from the radula. × 390.

The "receptaculum seminis" is connected by a short duct with the genital cloaca and receives the spermatozoa at the time of copulation. Of course the size of this vesicle varies according to the season and according to whether or not it is full of spermatozoa.

Breeding habits.— In general the breeding season of our species extends from the last of June to the first of September. There seems to be considerable variation in the time when the egg laying begins, in 1897 the capsules were first found July 9th. In 1898 none were found until July 25th. Then three were found which had been laid within thirty-six hours. In 1900 collecting was begun July 10th and capsules were found which must have been layed as early as June 25th, judging from the fact that the embryos had already left some of the capsules and were leaving others. However, the animals lay most abundantly between July 15th and August 15th. The egg capsules may be found scattered through the eel grass and algæ on the edges of the pond, or lagoon, but each capsule is attached to grass or algæ from two to six feet below the surface of the water. Apparently the animals congregate in favorable spots to lay their eggs. In one place in the eel pond, where the water is about three feet deep at low tide, over five hundred capsules were collected in ten days within an area about ten feet square. During the same period repeated trips were made to various parts of the pond, but only a very few capsules were found.

On the sandy bathing beach previously mentioned the animals lay in the same place from year to year. Here there is a small patch of eel grass in about three feet of water; in and around this patch the eggs are laid in great numbers. In this locality the capsules are attached either to the eel grass or, as in most cases, simply to the sand. The sandy bottom slopes out gradually for about one-fourth of a mile, merging finally into a muddy bottom. I have never dredged here, either before or after the breeding season, so I do not know where Haminea stays during other seasons; but I have dug down into the sand, both before and after the laying season, and have never been able to find any of the animals. It is difficult to ascertain where Haminea lives at other times than the breeding season, but the fact that it cannot be found in shallow water except at this time seems to show that it migrates into deeper water. This idea is also supported by the occurrence of Haminea in thirty feet of water in the Big Harbor, and by the statement of Verrill ('72) to the effect that, "A specimen of winter flounder

(*Pseudopleuronactes americanus*) caught at Wood's Holl in August, contained a large number of the shells of Bulla solitaria." The winter flounder is dredged in the vicinity of Wood's Holl at a depth of about fifteen to thirty feet, and is mentioned by Verrill as devouring Bulla in large numbers. Haminea has been dredged in May in Hadley Harbor at a depth of twenty-five feet. These facts would tend to show that its natural habitat for the most of the year is the deeper water. A further proof that *H. solitaria* lives in deep water except during the breeding season is supplied by the following facts: August 28, 1900, Dr. C. V. Wilson while skimming the surface water with a fine mesh net near Edgartown, secured a large number of *H. solitaria*. They all died during the first night although they were placed in a small aquarium. The time that these individuals were collected was after the usual egg laying periods for the forms that live in the vicinity of Wood's Holl. When taken, they were evidently migrating into the deep water. The observations of Verrill and those of Wilson seem to show conclusively that *H. solitaria* is a deep sea dweller except for about six weeks, when it takes up temporary quarters in some favorable place in shallow water.

During the first two summers that *H. solitaria* was under my observation I was unable to discover any evidences of copulation, owing to the fact that early in the season I did not have in the laboratory any considerable number of animals; but in the summer of 1900 I had in the laboratory about forty animals at one time and was able to make observations on copulation. The habit which these molluscs have of crawling over one another and of collecting into a pile, concealed the fact and method of copulation for a long time. One day, however, I noticed two animals apparently copulating, the genital grooves were slightly extended and came together, from one the penis protruded into the genital groove of the other. The animal receiving the penis laid a mass of eggs eight hours after the copulation, the other one did not lay. In a second case of copulation the animal laid after the lapse of thirty-six hours, but this was an unusually long time and probably due to the unnatural conditions surrounding it. In the time that elapses between the period of copulation and deposition, *H. solitaria* is similar to many of the nudibranchs (Smallwood :03).

The question arose as to whether or not copulation took place after laying; in the three cases that I was able to observe copulation did take place after one of the animals had laid but I was unable to observe it between animals both of whom had already laid. Fresh Haminea were collected, put into separate dishes, and kept there for three days; during this period they did not lay; then specimens which had copulated and laid were put in with these, copulation followed in each case in about an hour and the animals laid in about twelve hours. Sections of the ovotestis before and after copulation prove the correctness of the above observations.

In copulation the animals do not uniformly assume any definite position in regard to each other. The genital groove opens on the right side just anterior to the lateral fold of the parapodium, thus obviating the necessity for an exact position. Copulation continues for about fifteen minutes.

This species lays a single gelatinous mass (Fig. 9) which is spherical, about three-quarters of an inch in diameter. Its contents are chiefly composed of albumen, which is secreted by the albumen gland. As soon as the albumen comes in contact with the water it swells by the rapid absorption of water, and thus affords a gelatinous protection for the egg. When the eggs first leave the genital groove they are in strings; in a few hours the strings lose their continuity and the eggs are scattered throughout the egg mass. It would be very difficult to count the eggs in a single mass. The size of the capsule varies considerably; as a rule those found on the eel-grass are about a third less in diameter than those laid on the bottom. The egg masses laid in the laboratory were often irregular in shape and much smaller than those collected from the pond. The specimens in confinement that laid small and irregular masses, often laid a second time without a second copulation. It takes from 40 to 50 minutes for an animal to lay a complete normal egg mass.

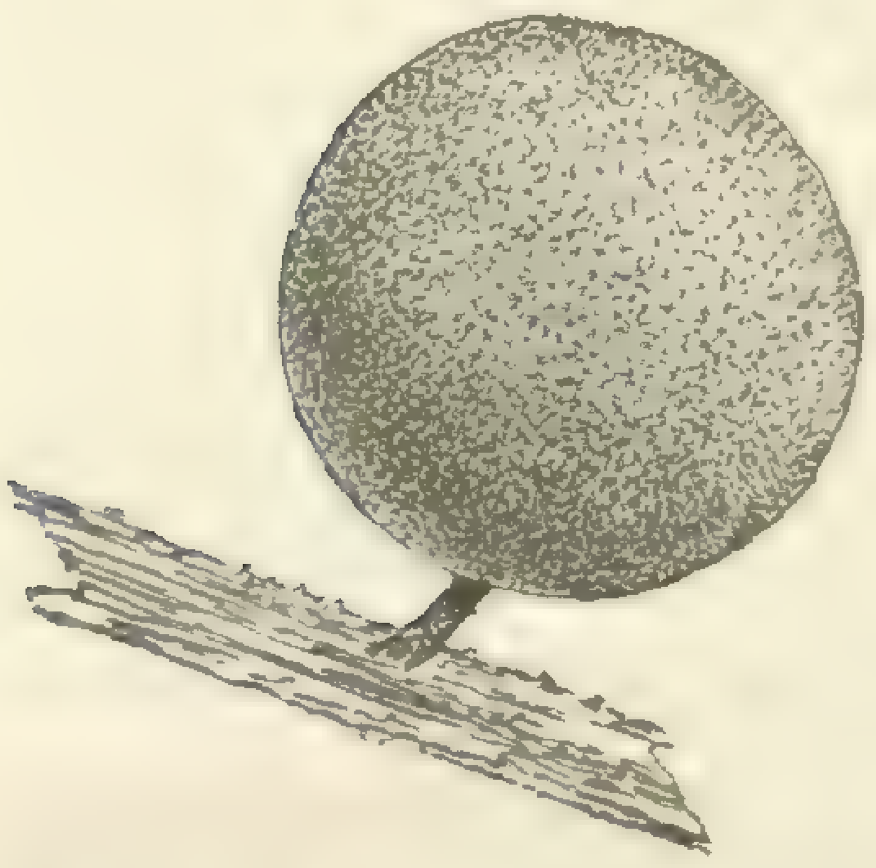

FIG. 9.—The eggs of *H. solitaria* are laid in a gelatinous mass, spherical in form, and attached to some foreign object. The drawing is natural size.

The living egg of *H. solitaria* is so small and so richly supplied with deutoplasm that satisfactory observations on the segmentation are impossible except in the early stages. The egg is spherical, enclosed within a thin structureless membrane. The size of the egg varies, the average is about .08 mm., being smaller than the eggs of Umbrella (Heymons, 93), Crepidula (Conklin, '97), Nucula (Drew, :01) and that of most molluscs that have been studied.

Before segmentation the polar differentiation of the egg is but slightly indicated, the yolk being almost uniformly distributed except in the region of the polar bodies. It has already been

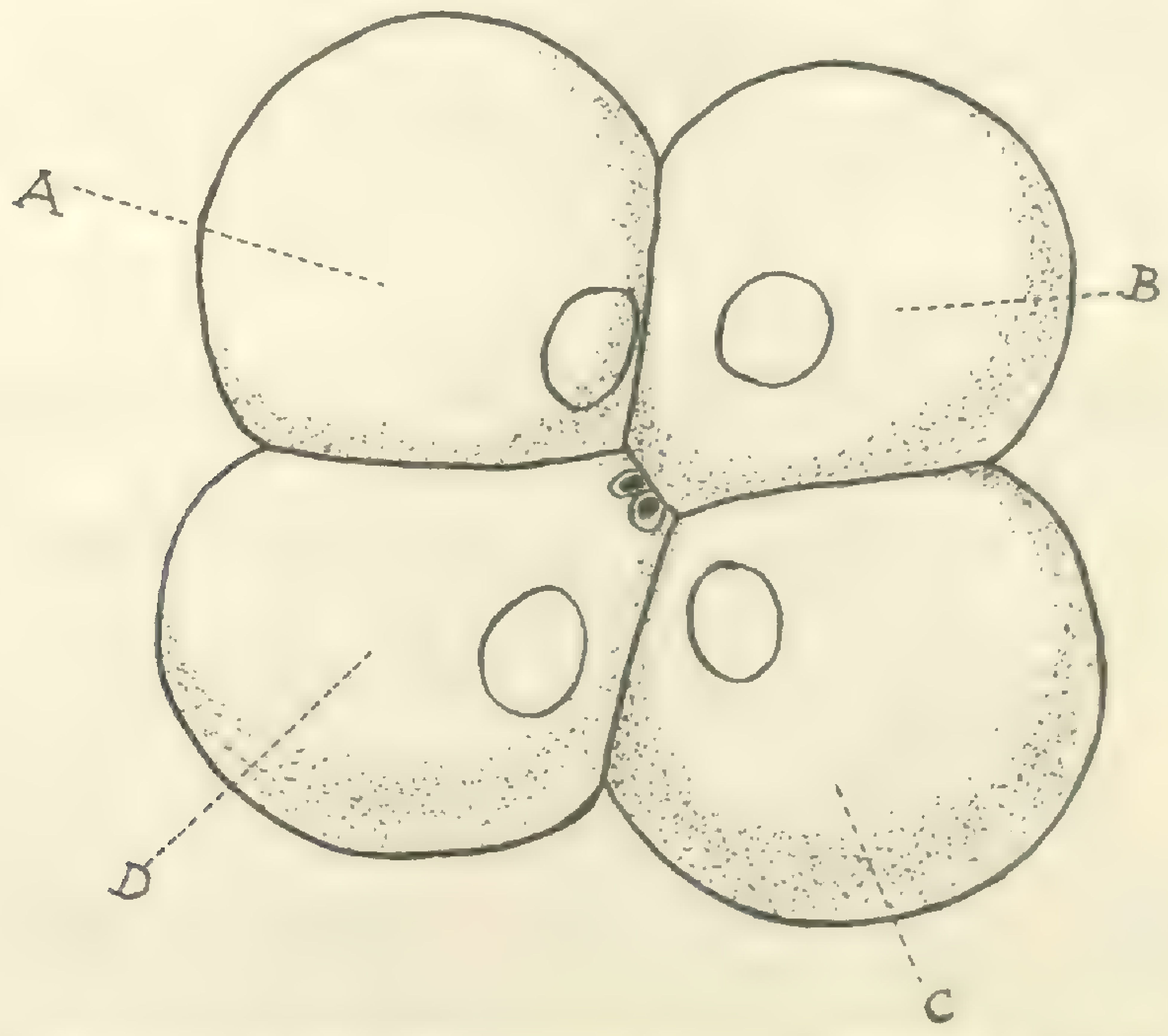

Fig. 10.—The four celled stage which shows the relation between the four blastomeres characteristic of Mollusca. × 275.

stated that it takes forty minutes for the animal to lay a mass of eggs. Within ten or fifteen minutes after each egg is laid the first polar body appears at the animal pole and thirty minutes later the second polar body can be seen. It happens occasionally that the first polar body is very large and may even contain yolk spheres.

The egg segments into two cells a half hour after the second polar body has appeared. In about thirty per cent. of the eggs observed, the first division of the egg did not divide it into two equal blastomeres, one being noticeably larger, a variation which

is similar to Umbrella (Heymons '93). Within thirty or forty minutes after the formation of the two celled stage, the four

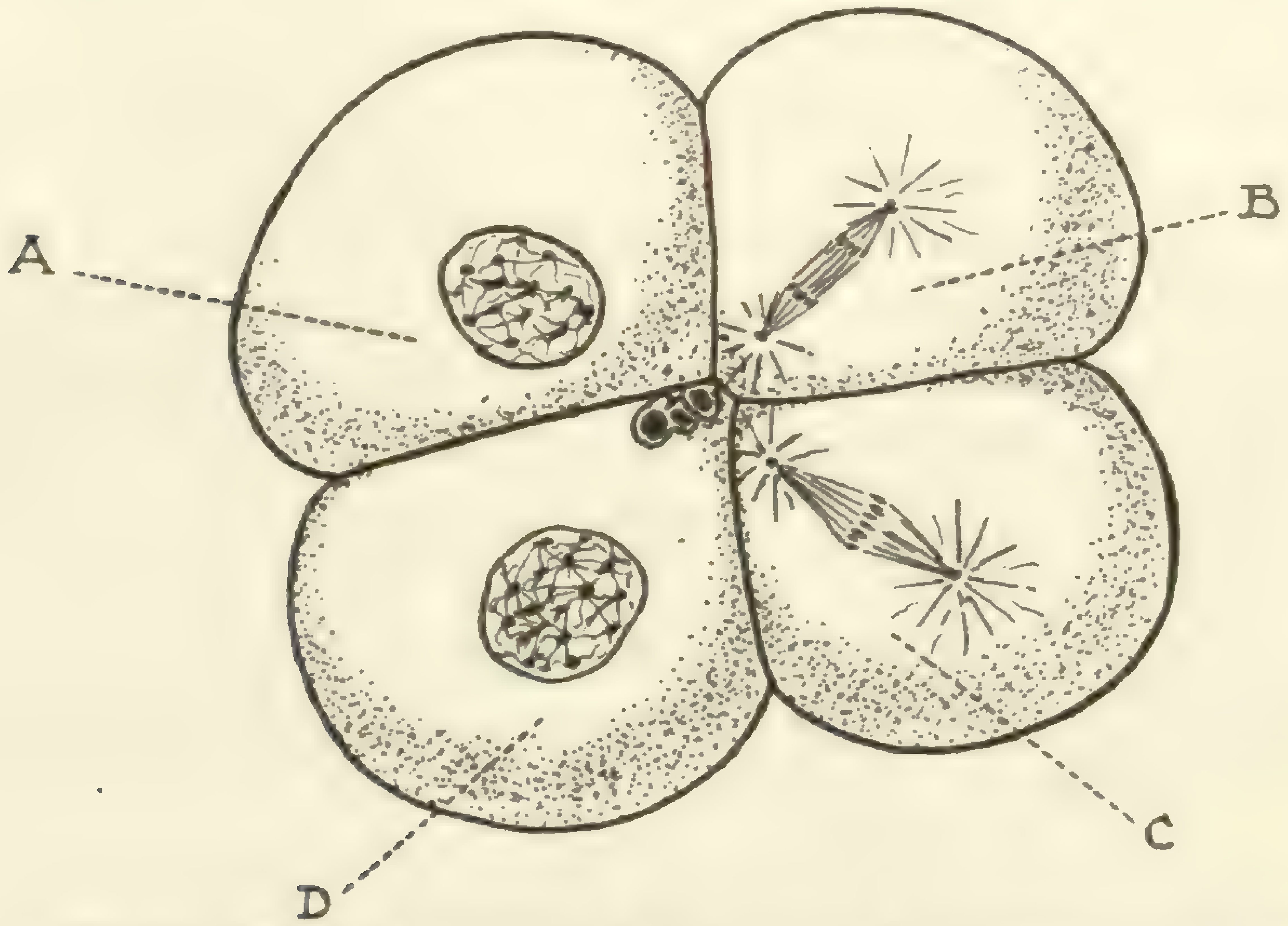

FIG. 11.—The four-celled stage preparatory to the formation of the first quartette of micromeres. × 275.

celled stage is formed. Just prior to the formation of the four celled stage, the spindles do not lie parallel which is an agreement with other molluscs and indicates a spiral division [1] (Fig. 10).

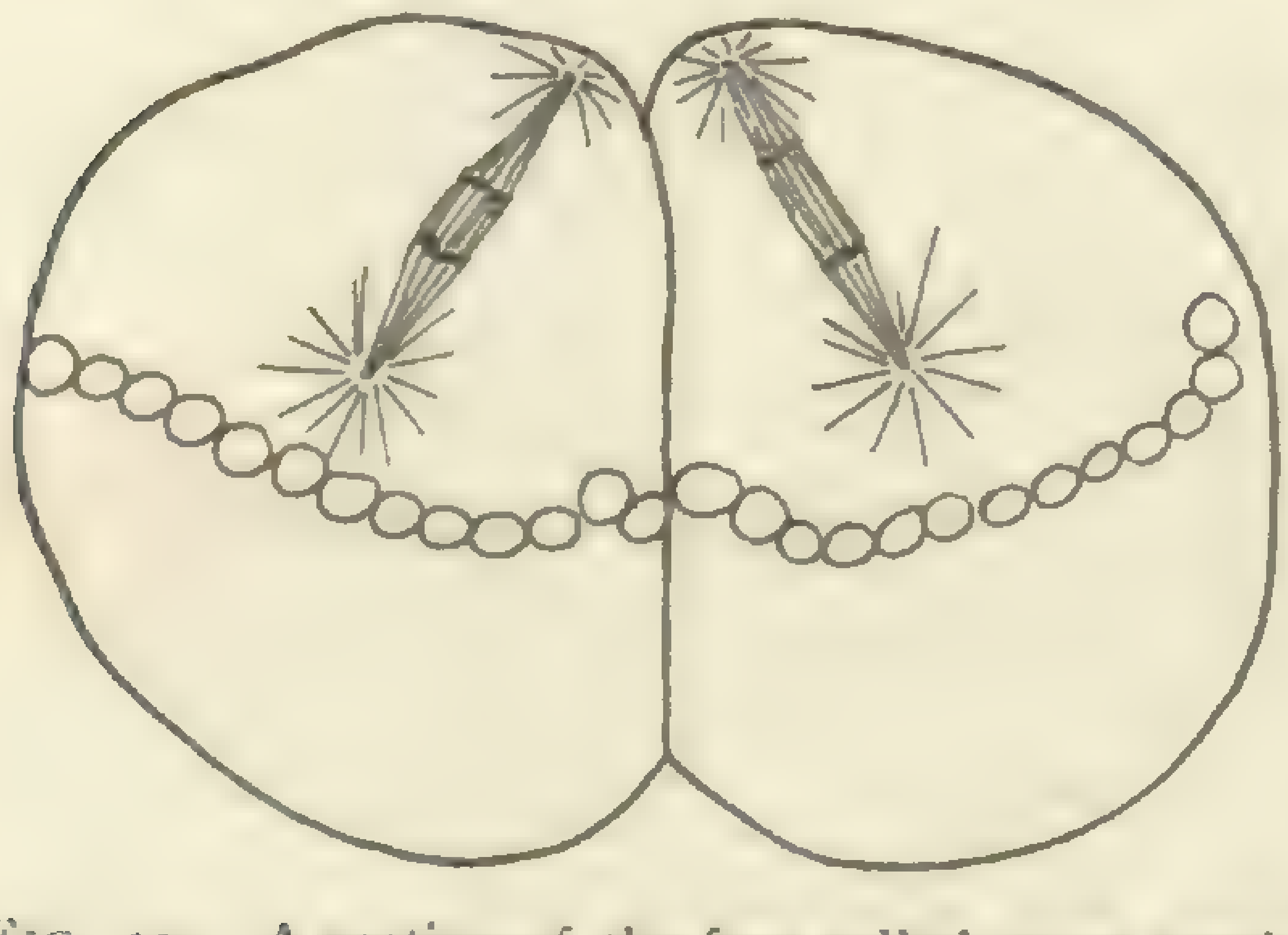

FIG. 12.—A section of the four celled stage passing into the eight celled stage to illustrate the position of the spindles when the micromeres are formed. × 140.

After not more than thirty minutes, the third cleavage separates the egg into two conspicuous parts, the protoplasmic micromeres and the deutoplasmic macromeres. These micromeres are considerably larger in comparison with the size of the macromeres than in many molluscs. The same is true for the two following quartettes of micromeres

[1] For a complete discussion of the method and significance of segmentation in Mollusca see Mark, E. L., Maturation, Fecundation, and Segmentation of Limax campestris. *Bull. Mus. Comp. Zool.* vol. 7. 1881. Conklin. E. G., The Embryology of Crepidula. *Jour. Morph.* vol. 13, 1897. Holmes, S. J., The early development of Planorbis, *Jour. Morph.* vol. 16, 1900.

which results in the complete envelopment of the macromeres at an early stage. The third cleavage is dexiotropic (Figs. 11, 12, 13, 14).

The time that intervenes between the formation of the second and third quartettes of micromeres is the same as that for the second and third cleavage. From this time on it was impracticable to follow the further cleavage stages on the living egg. Stained preparations confirmed the observations made on the living egg.

The second quartette of micromeres is formed by the fourth cleavage which takes place in an anti-clockwise direction, the

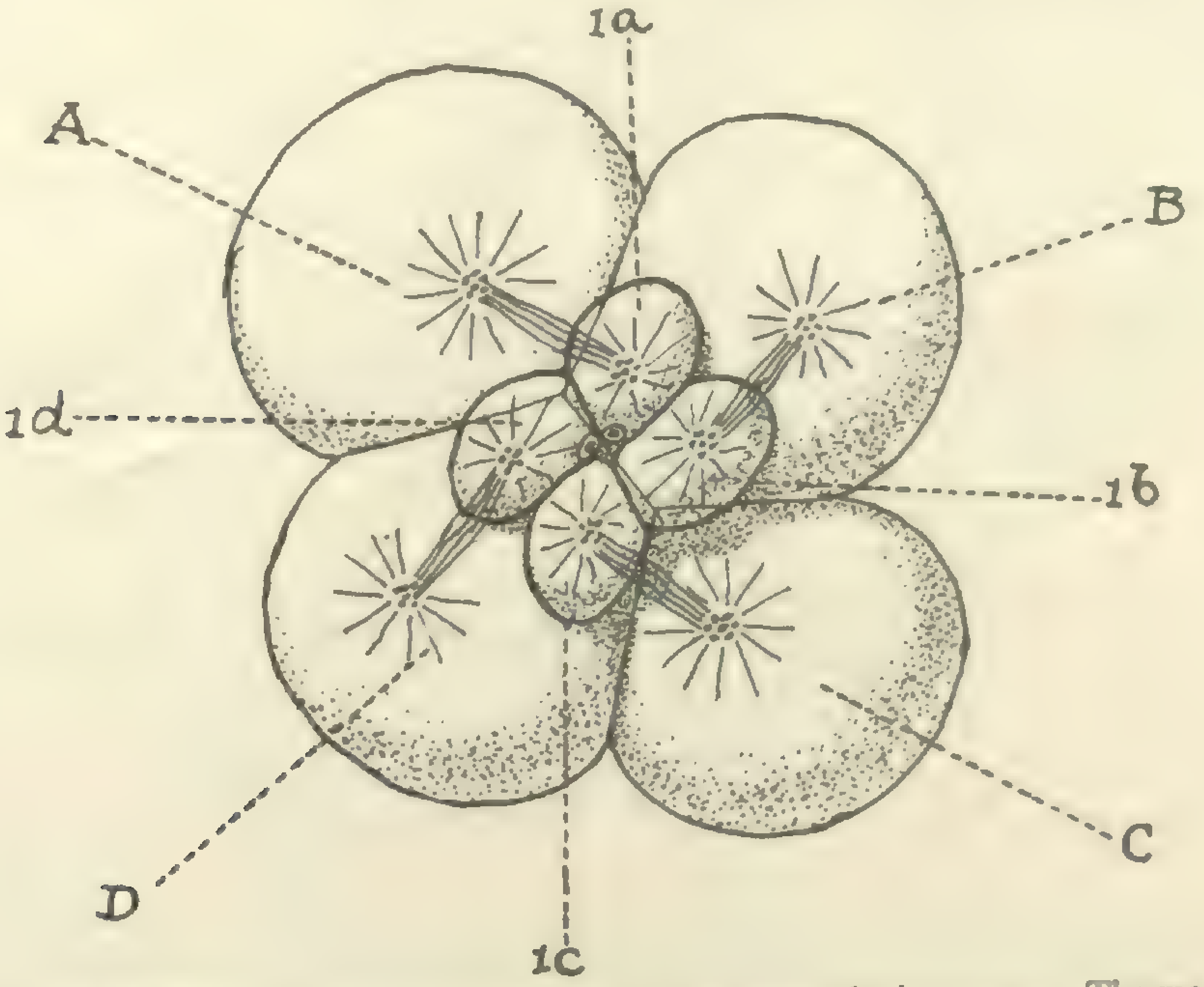

FIG. 13.—The telophase in the formation of the first quartette of micromeres. The movement is dexiotropic.

cells taking a position alternating with the cells of the first quartette (Fig. 15). The next cells to undergo segmentation are the first micromeres formed, segmentation takes place in a læotropic direction giving rise to the turret (trochoblast) cells (Figs. 15, 16); immediately after, indications of division in the second quartette of micromeres and the macromeres are evident. The egg sketched shows eight complete spindles in the metaphase. The spindles occurring in the macromeres participate in the formation of the last quartette of micromeres, the movement being in a right handed spiral. Soon after the above described

changes have taken place the macromere which is designated by the letter D divides independently of the three other macromeres into two cells of unequal size but both containing yolk spheres. The smaller cell is concerned in giving rise to the mesoblastic bands and is entirely covered above by the micromeres.

It can be seen from the brief description of the early segmentation stages and the accompanying sketches that *Haminea solitaria* does not exhibit any segmentation phenomena other than those characteristic of mollusca. The subsequent cleavage

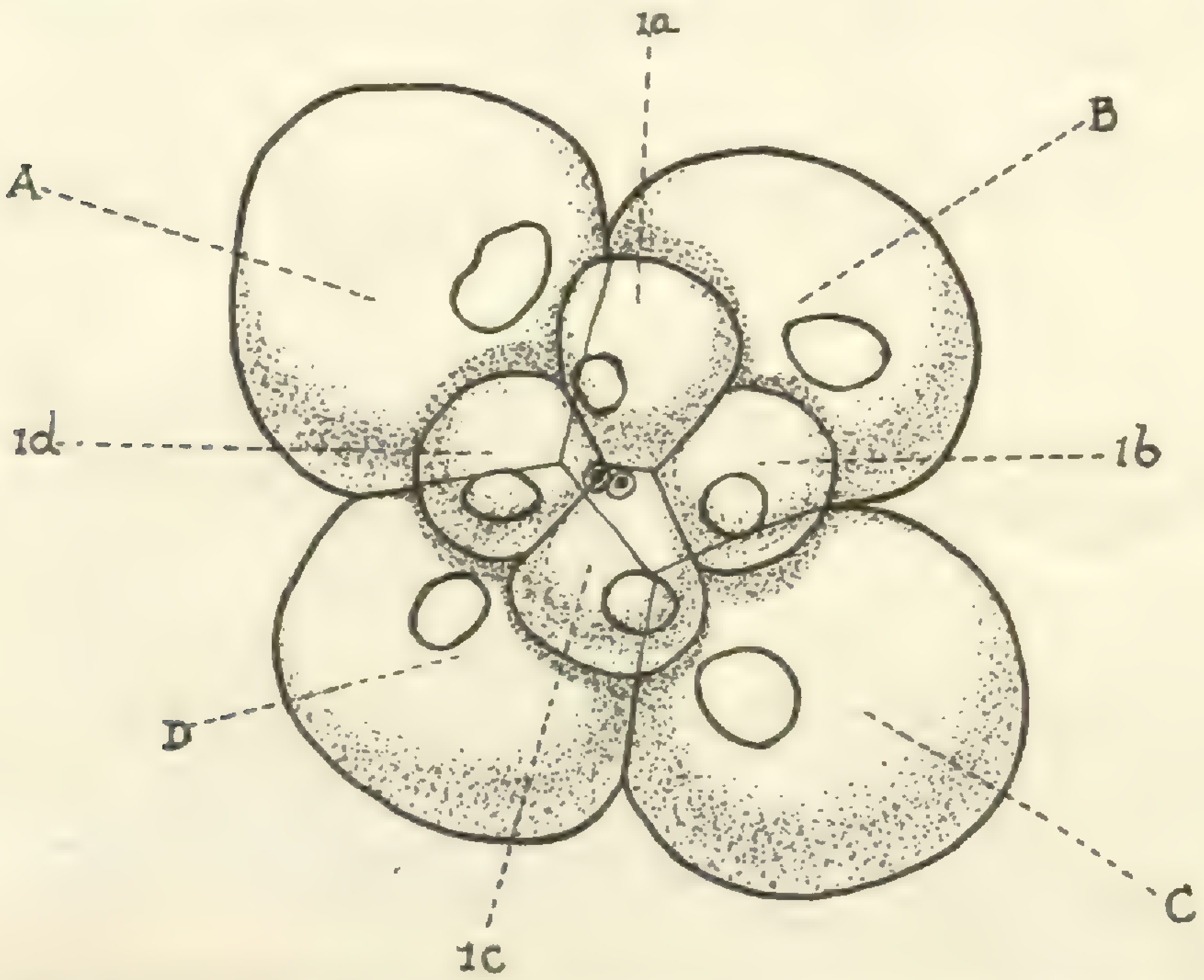

FIG. 14.—The eight celled stage fully formed showing the position of the micromeres above the furrows of the macromeres. × 275.

stages have been followed sufficiently to indicate that they are in agreement with related forms that have been described heretofore.

The embryo usually begins to move in the egg capsule at the end of the seventh day; the cilia on the mantle border are well differentiated and can be seen in motion. It is difficult to ascertain the exact length of time the embryo remains in the egg capsule but I have known it to continue there for a week. In most of the egg masses that have been under observation the embryos have died before becoming free swimming individuals although some were immediately placed in aquaria or in the

eel pond in bottles closed with several thicknesses of cheese cloth. In placing the embryos in their natural environment, it was hoped that it would be possible to determine the changes taking place between the embryo and the adult. Although repeated experiments were made in various parts of the eel pond, no satisfactory results were obtained and I am unable to state how the transition from the embryo to the adult takes place.

During the summer of 1899 a number of pressure experiments were tried for the purpose of determining the effect on segmentation and the subsequent history of the embryo. The fact that the eggs are surrounded by a great mass of albuminous

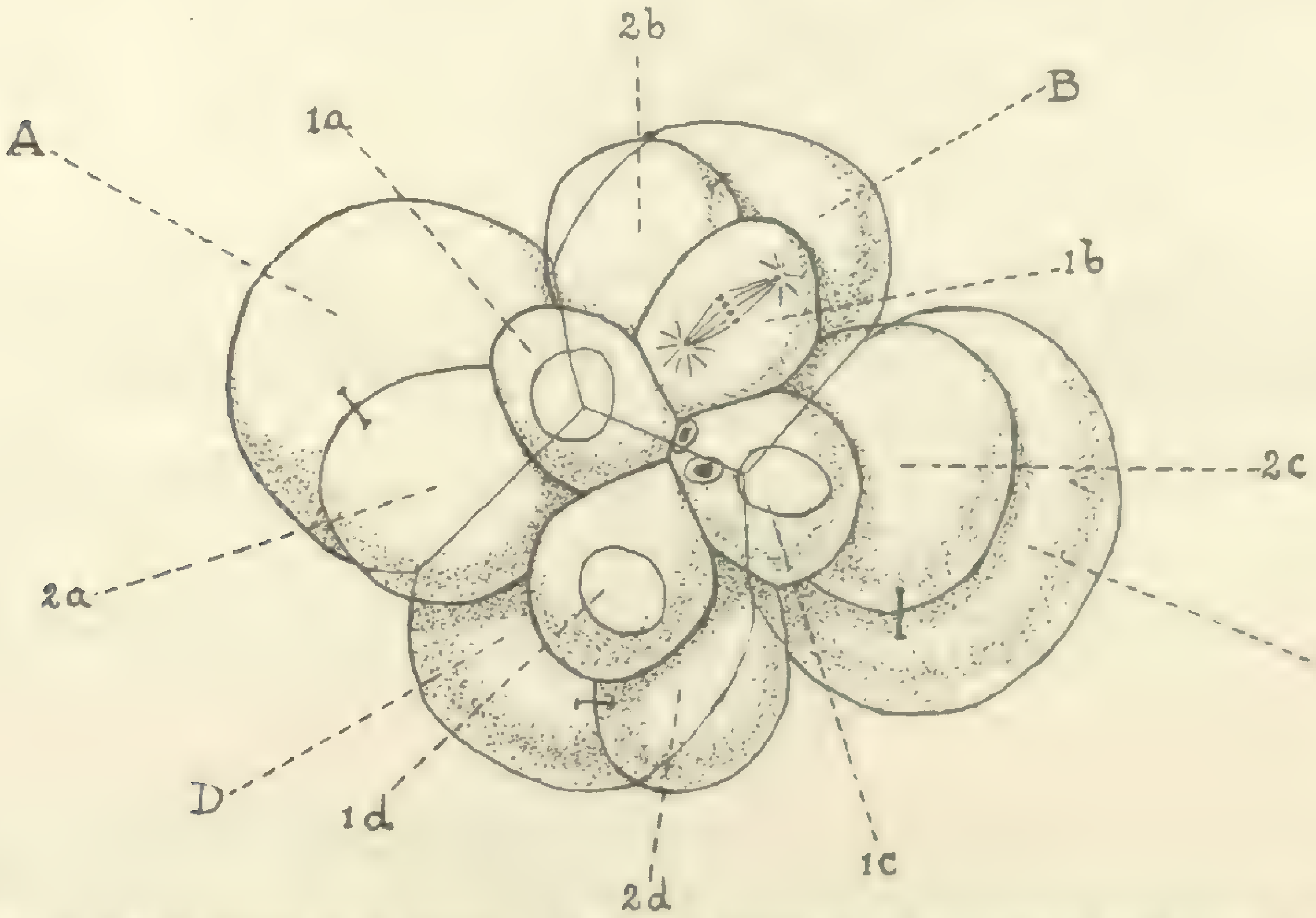

FIG. 15.—The twelve celled stage. The second quartette of micromeres was formed by a laeotropic movement. One cell, 1b, is undergoing segmentation which will result in the formation of a turret cell. × 275.

material made it easy to apply light pressure. A small number of eggs were placed on a slide and covered by a second slide, the amount of pressure was regulated by passing a small rubber band around the slides. The eggs were taken in the one celled stage after the polar bodies had formed; they were left under pressure two hours and the changes which took place during the period were carefully noted. I took pains to see that all of the eggs were forced to segment in an irregular manner. After the pressure was removed the eggs were placed in the aquarium in a bottle which was stoppered with cheese cloth. Although a

number of experiments of this kind were tried with different degrees of pressure I was not able to get any normal embryos. A few abnormal embryos were reared but they lived but a few days. It hardly seems that it will be possible to get any fruitful results from pressure experiments on the eggs of *H. solitaria* for these further reasons: eggs in the egg masses broken during collection develop abnormally, probably because the sea water gains access to them; eggs laid in imperfect egg masses in the laboratory frequently develop abnormally; occasionally I have

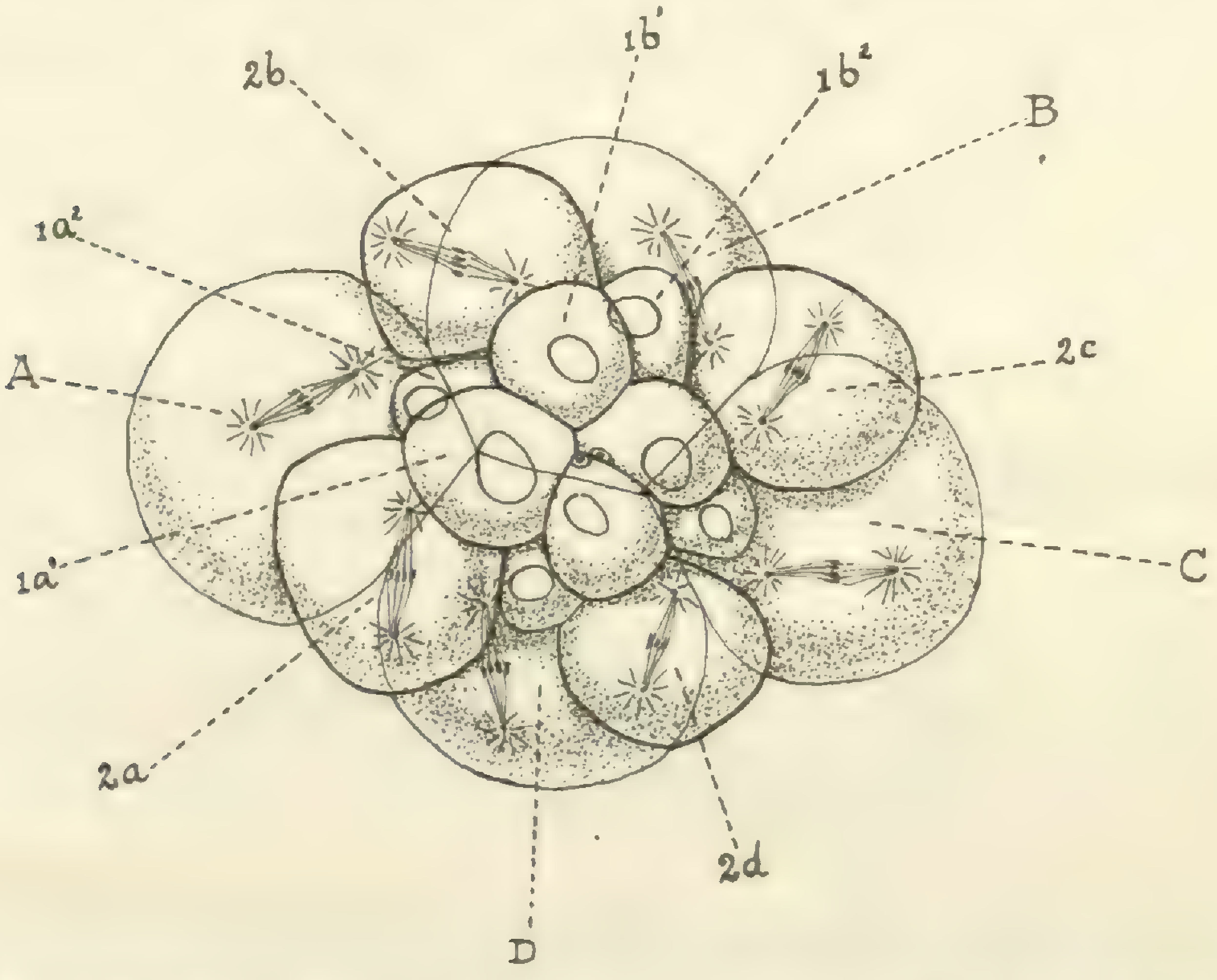

FIG. 16.—The sixteen celled stage. The first quartette of micromeres have given rise to four turret cells, 1b². The third quartette of micromeres is forming by a dexiotropic movement. The second quartette of micromeres is the process of division. × 275.

collected what appeared to be perfect egg masses and found that the segmentation was very irregular, keeping these eggs under observation, I found that they invariably died in a short time; some apparently normal egg masses have been found to contain eggs in all stages of segmentation from the one celled to the thirty celled stage.

In brief then to summarize: The Techtibranch mollusc, first described by Say, and subsequently by Totten, Verrill, and others, should, according to Pilsbry, properly be regarded as *Haminea solitaria.* The dental formula is ∞. 1 ∞. The egg

laying period extends from the middle of June to the last of August during which time the adults migrate from the deep water into shallow ponds and lagoons. The eggs are laid in a gelatinous mass, spherical in form, attached to eel grass, algæ, stones, sticks, etc. The eggs pass from the one celled stage to the free swimming embryo in seven days. The method of segmentation of *Haminea solitaria* is in close agreement with the other mollusca. No positive results were obtained from attempts to produce abnormal segmentation.

Zoölogical Laboratory, Syracuse University,
November 15, 1903.

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NOTES AND LITERATURE.

GENERAL BIOLOGY.

Mendelism and Cytology.[1] — Guyer's doctor's thesis written in 1900 but printed and distributed in the latter half of 1903 is remarkable for its "anticipation" of Mendel's law of purity of the germ cells, the outcome, unlike Mendel's results, of a cytological study. He first describes the course of spermatogenesis in normal pigeons. The spermatogonia (the ancestral sperm cells immediately preceding the reduction stages) contain 16 chromosomes which are split in the cell division that forms the primary spermatocyte. As the primary spermatocyte grows, synapsis, or a fusion of the chromosomes in pairs, occurs; and this Guyer interprets as the conjugation of maternal and paternal chromosomes. Eight thick rings are formed which break equatorially in the division by which the secondary spermatocytes are produced. When the secondary spermatocytes divide to form the young spermatozoa only four chromosomes are to be seen. These chromosomes Guyer regards as quadrivalent and he suggests that "reduction" takes place when they divide.

He suggests that the reduction division of the four-fold chromosomes may be in any plane and so varying combinations of maternal and paternal qualities will go to each spermatozoon. Thus it might happen that in the division the maternal and paternal qualities were segregated (and this he regards as the prevalent result in hybrids); or it might happen that some of both the maternal and paternal chromatin went to each spermatozoon. The "purpose" of the formation of the quadrivalent chromosomes is to give greater variability.

In respect to hybrid pigeons, Guyer notes that the offspring of the common brown ring dove mated with a white ring dove are brown. The offspring of these brown hybrids are either white or brown and the latter color predominates. The author says (p. 36): "This points to the conclusion that in the brown birds we may have

[1] Guyer, Michael F. *Spermatogenesis of Normal and of Hybrid Pigeons.* A Dissertation, etc. University of Chicago, Chicago; 1900. 61 pp., 2 (double) plates. [Distributed (and printed?) 1903.]

both intermediate forms like the hybrids of the second generation and forms which have reverted to the brown grandparent, as the white doves have seemingly returned to the white grandparent." Here we have a clear recognition of what Mendel calls dominance! Also, this, (p. 48): "If a spermatozoön and an egg containing characteristics of the same species unite, then the reversion will be to that of the species; if a sperm cell containing the characteristics of one species happens to unite with an ovum containing characteristics of the other species, then the offspring will be of the mixed type again. By the law of probability the latter will be the more prevalent occurrence, because there are four combinations possible, and two of the four would result in the production of mixed offspring, while only one combination could result in a return to one of the ancestral species." Here we have even the quantitative part of Mendel's law expressed in 1900!

The foregoing Mendelian generalizations are suggested by the behavior of the hybrid germ cells in the spermatogenic stages. The mitoses are frequently abnormal — two spindles lying side by side, owing to the fact that the chromosomes are segregated in different parts of the cell. This segregation suggests an incompatibility between the chromosomes of the two species — and it results in "pure" germ cells — with the parental qualities segregated.

Finally, the all too brief chapter of suggestions will repay careful study. It is regrettable that so notable a contribution to the mechanism of heredity should have been so long delayed in appearing.

C. B. D.

Inheritance of Acquired Mental Characteristics.[1] — A Chicago solicitor of patents has written a book on heredity that is bold and in many respects crude, but which presents so many facts that it warrants respectful consideration. The subject is the control of the intellectual quality of the offspring by the intellectual activity of the parents. The thesis is that the descendants of intellectually active parents inheret the latter's activity so that, within limits, the more active during a given time the parents have been, or the longer the time of their activity, the more intellectually active the offspring, the greater their chance of achieving eminence. It is nothing new, of course, that the offspring of intellectual or successfully active people are especially apt to have eminent progeny, but it is rather new to

[1]Redfield, C. L. *Control of Heredity.* A Study of the Genesis of Evolution and Degeneracy. Chicago, A. C. Clark, 1903. 8vo. 343 pp., illustrated.

be told that of the progeny of such eminent people the younger sons are more likely to be eminent than the older sons; or conversely, that eminent men, in general, particularly when not sons of eminent men are sons of old men.

To prove the thesis stated in the last paragraph it would be necessary first of all to find the average age a large random sample of mothers and of fathers of a given race and time at the birth of all their children and then to show that eminent people (using as a measure of eminence some arbitrary standard such as the average number of lines in the biographical descriptions in a number of encyclopedias) were born of parents clearly older than the average of parents of that race and time. But even this would not be wholly satisfactory. It would be better to compare the average eminence of the earlier and the later born of pairs of brothers. If the average eminence of the later born brothers exceeded that of the earlier born by several times the probable error then the greater chance of eminence of younger sons could be said to be demonstrated. But even if the younger sons showed a clearly greater eminence, still we could not assert that this greater eminence was due to inheritance of acquired intellectual activity of the parents rather than to the possible superior training of later sons.[1] Now Mr. Redfield has not treated his statistics of eminence in relation to birth rank with sufficient care; he is convinced of the truth of his theory; and he uses all of the art of a skillful lawyer to prove it.

Mr. Redfield got a standard average age of Caucasian parents in general from the Redfield genealogy, which indicates that 50% of children are born from fathers under 33 years and mothers under 29 — these ages are taken as his standard although he thinks them a trifle high for Caucasians in general. He compares with this standard the father's age of eminent men at the time of the latter's birth, gleaning his facts from encyclopedias, and finds many cases of sons of old men. He devotes one chapter to "The Hall of Fame" men. He finds among these many cases of exceedingly old parentage. For instance when Franklin was born his father was 51; and the total interval in three generations is 51 + 57 + 70 = 178 years. On the other hand the average birth rank of Eli Whitney's male ancestors was 30 and for 25 Hall of Fame men the median paternal birth rank is 35.5 years, not much above Redfield's standard.

[1] To avoid the possible influence of superior training of younger children records of trotting horses or milk-cattle would be superior to records of men. Mr. Redfield thinks his theory confirmed in trotting horses.

The argument is weakened by including the birth ranks of Joseph, Moses, David and Solomon! We have little reliable information concerning the ages of the ancestors of these men. Also, our confidence in Mr. Redfield's critical ability is terribly shaken by his comparison of maternal impressions to mimicry, and by his attempting to account for the intellectual inferiority of the lower animals solely on the ground of their shorter generations.

Despite, however, all the crudities of the book we cannot deny that it contains suggestions and that many of the conclusions cannot, in our present state of knowledge, be refuted. The work should incite to further and more careful investigation to confirm or refute Mr. Redfield's theory, or, rather, to see if statistical evidence supports the hypothesis of the inheritance of acquired dynamical qualities.

C. B. D.

BOTANY.

Notes.— Lieforung 29–30 of Ascherson and Gräbner's *Synopsis der mitteleuropäischen Flora* deals with Cyperaceæ, Araceæ and Palmæ, — among the latter characterizing American and other foreign species that are hardy in cultivation.

No. 26 of the new series of "Contributions from the Gray Herbarium of Harvard University," forming Vol. 39, No. 11, of the *Proceedings of the American Academy of Arts and Sciences*, is a revision of the genus Flaveria, by J. R. Johnston.

Under the title *Arkiv för Botanik*, a new serial has been launched by the K. Svenska Vetenskaps-Akademie. Several of the papers of the opening number are of interest to American botanists.

After a long interval, parts 3 and 4 of *Muhlenbergia* has appeared, and contain descriptions of a number of western phanerogams by Heller and Congdon.

The supplement to the *Index Kewensis*, in fascicle 3, reaches Physaria.

The embryology, etc., of *Sequoia sempervirens* are discussed by Lawson in *Annals of Botany* for January, which also contains a historical account of the structure and morphology of ovules, by Worsdell.

"The Flow of Maple Sap" is the subject of *Bulletin No. 103* of the Vermont Agricultural Experiment Station.

The influence of lime on plant growth is discussed by Wheeler and Adams in *Bulletin 96* of the Rhode Island Agricultural Experiment Station.

Vol. 4, no. 3 of the *West Indian Bulletin* is devoted to cotton.

The extent of variability in Eucalyptus is considered by Maiden in Vol. 36 of the *Journal and Proceedings of the Royal Society of New South Wales.*

A systematic-anatomical study of the leaf in Acer, with special reference to the late elements, by Warsow, has been issued from the Fischer press, of Jena.

An anatomico-biological thesis on seeds of Podalyrieæ, by Lindinger, has been issued from the Fischer press, of Jena.

An interesting thesis on the anatomy and biology of the fruit and seed of certain aquatics, by Fauth, has been issued from the Fischer press, of Jena.

The principal species of wood and their characteristic properties are described by Snow in an illustrated volume recently issued from the press of John Wiley and Sons of New York.

An illustrated account of Persian dates and their introduction into America, by Fairchild, forms *Bulletin No. 54* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

Germinating spores in a fossil fern sporangium are described by Scott in *The New Phytologist* of January 27.

A preliminary notice on fertilization, alternation of generations and general cytology of Uredineæ is published by Blackman in *The New Phytologist* of January 27.

New or unrecorded Australian fungi are being published by McAlpine in the current *Proceedings of the Linnean Society of New South Wales.*

An article on the genus Harpochytrium in the United States, by Atkinson, is published in the *Annales Mycologici*, for November.

A paper on Italian Hypogaeæ, by Mattirolo is separately issued by the *Accademia Reale delle Scienze di Torino.*

Bulletin 21 of the Boston Mycological Club is devoted to *Agaricus subrufescens*.

Accounts are given, in the January *Journal of the New York Botanical Garden*, of the laboratories of the institution, including that in Jamaica, and of the Carnegie desert laboratory at Tucson.

A well illustrated account of the Desert Botanical Laboratory of the Carnegie Institution, and of the desert regions of the Southwest, by Coville and MacDougal, constitutes *Publication No. 6* of the Institution.

A note in the *Journal of the Kew Guild* for 1903, shows that in 1902 1,323,376 persons visited the famous botanical gardens at Kew, the average for each of the previous ten years being 1,355,503.

Ramírez, in *Anales del Instituto Médico nacional*, vol. 6, no. 2, publishes notes on some of the manuscript icones of Sessé and Mociño.

"The Book of Herbs," by Lady Rosalind Northcote (John Lane, London and New York, 1903), is a tasty and interesting little book, well illustrated, and with a portrait of Parkinson for frontispiece.

Those who care for old books will find interest in a supplementary catalogue of the Sturtevant Prelinnean Library of the Missouri Botanical Garden, by Hutchings, published in the 14th *Report* of that institution.

An account of the botanical work that has been done in the Philippines, with a bibliography, is given by Merrill in *Bulletin no. 4*, of the Bureau of Agriculture of the islands.

The third part of vol. 2 of Wood's "Natal Plants," devoted to grasses, and the first part of vol. 4 of the same work, containing gamopetalæ, have recently been issued.

A popular Sketch of Hawaiian botany, by Morrison, is contained in *Floral Life* for November.

Some views of the vegetation of the Dismal Swamp accompany an article on the proposed ship canal through it, in *The American Inventor* of December 1.

Dr. Holm contributes some Notes on Canadian Species of Viola to *The Ottawa Naturalist*, for December.

Perrot and Guérin publish an account of the Didiereas of Madagascar, with habit illustrations, in the *Journal de Botanique* of August–September.

A critical revision of Gossypium, by Aliotta, has been separately printed from vol. 5 of the *Annali della R. Scuola Sup. d'Agricoltura in Portici.*

Andean cacti of interest are being described by Schumann in current numbers of the *Monatsschrift für Kakteenkunde.*

The Indian Species of Polygonum and reviewed by Gage in vol. 2, no. 5, of the *Records of the Botanical Survey of India*, dated Sept. 14.

Part XX of Holm's Studies in the Cyperaceæ is contained in *The American Journal of Science* for December.

The comparative anatomy and phylogeny of Sequoia are discussed by Jeffrey in vol. 5, no. 10, of the *Memoirs of the Boston Society of Natural History*, issued in November.

A new Alstonia, yielding rubber, is described from New Caledonia by Schlechter in *Der Tropenpflanzer*, for November.

Shade trees, etc., adapted to New Mexico are considered by García in *Bulletin no. 47* of the Agricultural Experiment Station of New Mexico.

An article on Conservation and Cultivation of Medicinal Plants, by Kræmer, is contained in the December number of the *American Journal of Pharmacy.*

An account of the grape-growing industry of the United States is contained in *The National Geographic Magazine*, for December.

Symbiosis of Volvox and Azotobacter is discussed by Reinke in the *Berichte der deutschen botanischen Gesellschaft*, vol. 21, Heft 8.

A discussion of soil temperatures and vegetation by MacDougal, is reprinted from the *Monthly Weather Review*, for August.

School Science, for December, contains a description of a new and cheap form of Auxanometer, by Lloyd.

An account of a seemingly bacterial disease of tobacco, by Stevens and Sackett, is given in *Bulletin no. 188* of the North Carolina Agricultural Experiment Station.

Some oddly grown trees are figured by Newcomb in *Floral Life*, for December.

President Seward's address before the Botanical Section of the British Association, at its recent meeting, is printed in *Nature* of October 8, and deals with the composition and distribution of the floras of the past, with reference to the corresponding phases of the flora of to-day.

Harshberger contributes to part 2 of the current volume of *Proceedings of the Academy of Natural Sciences of Philadelphia* a paper on Mutations of *Hibiscus Moscheutos* and one on Form and Structure of the Mycodomatia of *Myrica cerifera*.

A spontaneous rapid vibratory movement of certain shoots of Eucalyptus is recorded by Tavares in *Broteria* of October 30, — which contains a number of other articles of botanical interest.

The propagation of plants is discussed by Corbett in *Farmers' Bulletin No. 157*, of the U. S. Department of Agriculture.

Data on autumnal coloring, as correlated with leaf deterioration, are contributed by Keegan to *Nature* of Nov. 12.

Anatomical studies of Potamogeton are applied to the classification of the species of this difficult genus by Raunkiær in a paper reprinted from Heft 3 of the current volume of *Botanisk Tidsskrift*.

An article by Fritsch on the Use of Anatomical Characters for Systematic Purposes is contained in *The New Phylologist* for October.

Fendlera rupicola is illustrated in *Curtis's Botanical Magazine* for November.

Ostenfeld and Raunkiaer, in Heft 3 of the current volume of *Botanisk Tidsskrift*, show that Hieracium, like Taraxacum, appears to be apogamic, — a peculiarity not shared by other genera of Cichoriaceæ experimented on.

The distinctive marks of *Catalpa speciosa* are figured and described by the Editor in *Arboriculture* for October.

A paper on *Asplenium Ruta-muraria*, by Christ, in *Hedwigia* of October 7, includes an analysis of North American forms.

Numbers of Lloyd's *Mycological Notes* published during the current year include studies of Catastoma, Mitremyces, Tylostoma, Secotium, etc., accompanied by a good many photograms.

A third supplementary list of the parasitic fungi of Wisconsin, by Davis, has been printed in advance from Vol. 14 of the *Transactions of the Wisconsin Academy*. A total of 661 species is now recorded.

Fascicle 4 of Sydow's Monographia Uredinearum carries Puccinia to species No. 1094.

A paper by Holden and Harper, on nuclear division and fusion in Coleosporium, is separately printed from Vol. 14, part I, of the *Transactions of the Wisconsin Academy*.

Taphria (or Taphrina) *cærulescens* forms the subject of *Bulletin No. 126* of the Alabama Experiment Station, by Wilcox.

Part 9 of Koorders and Valeton's Additamenta ad Cognitionem Floræ Arboræ Javanicæ. forms No. 61 of the *Mededeelingen uit 's Lands Plantentuin*, published by Kolff of Batavia.

A primer of forestry, by Pinchot, constitutes *Farmer's Bulletin No. 173*, of the U. S. Department of Agriculture.

A popular account of broom corn, *Sorghum vulgare*, by Hartley, forms *Farmers' Bulletin No. 174*, of the U. S. Department of Agriculture.

A reprint of Schöpf's "Materia Medica Americana" (1787) constitutes *Bulletin No. 6* (Reproduction Series No. 3) *of the Lloyd Library*.

Palaquium Supfianum, a new Gutta-Percha plant of New Guinea, is described and figured by Schlechter in *Der Tropenpflanzer* for October.

A popular illustrated account of the pulque and mescal Agaves of Mexico is published by Dodge in the *Scientific American* of September 19.

The Journals.— *American Journal of Pharmacy*, January: — Lloyd, History of *Echinacea angustifolia*; Schneider, Gardens of Medicinal Plants.

The Botanical Gazette, December: — Transeau, On the Geographic Distribution and Ecological Relation of the Bog Plant Societies of Northern North America; Berry, Aralia in American

Paleobotany; Ganong, Vegetation of the Bay of Fundy Salt and Diked Marshes (concluded); Eastwood, Notes on Garrya with Descriptions of New Species and Key; Bergen, Transpiration of *Spartium junceum* and other Xerophytic Shrubs; and Atkinson, *Geaster leptospermus* — a correction.

Botanical Gazette, January: — Wylie, Morphology of *Elodea canadensis*; Newcombe and Rhodes, Chemotropism of Roots; Weld, Botanical Survey of the Huron River Valley — II, A Peat Bog and Morainal Lake; Godding, Southwestern Plants; Coker, Selected Notes — III.; and Farmer, On the Interpretation of the Quadripolar Spindle in the Hepaticæ.

The Bryologist, January: — Harris, Lichens–Peltigera; Miller, *Pogonatum urnigerum*; Grout, Notes on Vermont Mosses; Holzinger, The Genus Hymenostomum in North America; and E. G. Britton, *Papillaria nigrescens*.

Bulletin of the Torrey Botanical Club, January: — Arthur, New Species of Uredineæ, Harper, Explorations in the Coastal Plain of Georgia during the Season of 1902; Murrill, The Polyporaceæ of North America — VI, The Genus Polyporus; Robinson, the Spines of Fouquieria.

Journal of Mycology, December: — Morgan, A New Species of Berlesiella; Whetzel, New Method of Mounting Superficial Fungi; Bates, *Puccinia Phragmitis* in Nebraska; Stevens, Poisoning by *Lepiota Morgani*; Ellis and Everhart, New Species of Fungi; Kellerman, Uredineous Infection Experiments in 1903, Minor Mycological Notes — II, and Notes from Mycological Literature — VII. A portrait of Atkinson forms the frontispiece.

Journal of the New York Botanical Garden, January: — Britton, The Tropical Station at Cinchona, Jamaica; MacDougal, Research Work in the Garden; and The Desert Botanical Laboratory of the Carnegie Institution.

The Ohio Naturalist, January: — Kellerman and Jennings, Report for 1902 on the State Herbarium, including Additions to the State Plant List; Schaffner, Poisonous and other Injurious Plants of Ohio (concluded).

The Plant World, December: — Baum, The Breadfruit — III; Safford, Extracts from the Note-Book of a Naturalist on the Island of Guam — XIII; Simpson, Effects on Vegetation of the Hurricane

in Florida; Crawford, Some interesting Plants formerly abundant near Germantown, Pa.; and Thompson, Boniato — a Tree or a Yam?

The Plant World, January: — Safford, Extracts from the Note-Book of a Naturalist on the Island of Guam — XIV; Roosevelt, Our Forest Policy; Tullsen, Notes from Pine Ridge Agency, S. Dak.; Dobbins, The Parsleys; Barrett, Correction and Comment; and Gorman, Oregon Wild Flowers in Need of Protection.

Rhodora, December: — Fernald, Pursh's Report of Dryas from New Hampshire; Ames, *Lobelia* × *syphilitico-cardinalis*; Collins, *Woodsia glabella* in Maine; Robinson, Records of Wolffia in Mass.; Rand, *Matricaria discoidea* in N. H.; Chamberlain, New Stations for Maine Plants; Pease, Trisetum in Andover, Mass.; Freeman, *Lycopodium selago* on Mt. Holyoke; Osmun, *Cuscuta trifolia* in Mass.; Harger, New Station for *Phaseolus perennis*; and Collins, On Corallorhiza and Taraxacum.

Rhodora, January: — Fernald, Two Allies of *Salix lucida*; Brainerd, Notes on New England Violets; Rehder, Pseudo-monoclinism of *Chionanthus virginica*; Wiegand, Some Notes on Galium; Seymour, A Newly Introduced Galium; and Hervey, Plants new to the Flora of New Bedford.

Torreya, December: — Britton, Cornelius Van Brunt (with portrait); Cavers, Explosive Discharge of Antherozoid in Hepaticæ; Earle, Key to the North American Species of Inocybe — II; Maxon, A Fern New to the United States; and Holm, Linnæus' Work on Ferns.

Torreya, January: — Stone, Physiological Appliances — I; Banker, Observations on *Phallus ravenelii*; Canby, Joseph Hinson Mellichamp; Berry, Primary Venation in Cinnamomum.

The *Transactions of the American Microscopical Society*, Vol. 24, contains the following articles of botanical interest: — Bessey, Evolution in Microscopic Plants; Hollis, Two Growths of Chlamydomonas in Ct.; Seawell, Method of Concentrating Plankton without Net or Filter; and Bessey, Structure and Classification of the Phycomycetes, with a Revision of the Families and a Rearrangement of the North American Genera.

The American Botanist, of September, contains the following: — Bailey, The Defences of Plants; Bradshaw, Collecting Seeds;

Saunders, Poison Ivy and its Extermination; Buchheister, Variations in the Common Polypody; Gilbert, The Jewel Weeds; and part 6 of the Editor's Botany for Beginners.

The Botanical Gazette for October contains the following articles: — Harshberger, An Ecological Study of the Flora of Mountainous North Carolina; Parish, Sketch of the Flora of Southern California (concluded); Ganong, Vegetation of the Bay of Fundy Salt and Diked Marshes, An Ecological study (continued); Atkinson, A New species of Geaster; Davis, Tilletia in the Capsule of Bryophytes; and Lyon, Two Megasporangia in Selaginella.

The Botanical Gazette, for November, contains the following: — Evans, *Odontoschisma Macounii* and its North American Allies; Ganong, Vegetation of the Bay of Fundy Salt and Diked Marshes; Harshberger, An Ecologic Study of the Flora of Mountainous North Carolina (concluded); Moore, Mitoses in the Spore Mother-cell of Pallavicinia; and Haug, Is Detmer's Experiment to show the Need of Light in Starch-making reliable?

Volume 10 of the *Proceedings of the Iowa Academy of Sciences* contains the following botanical articles: — Pammel, Ecological Notes on the Vegetation of the Uintah Mountains; Weems and Hess, Chemical Composition of Nuts used as Food; and Fitzpatrick, The Scrophulariaceæ of Iowa.

The *Proceedings* of the second meeting of the *Iowa Park and Forestry Association*, recently distributed, contain a number of articles of botanical interest.

The *Journal of the New York Botanical Garden*, for November, contains the following: — Britton, Report on Cuban Exploration; Lloyd, Report of a Botanical Expedition to the Island of Dominica; and Nash, Report on Exploration in Hayti.

A new publication, "Leaflets of Botanical Observation and Criticism," has been launched by Professor E. L. Greene. The first signature is dated Nov. 24, 1903.

The Plant World, for November, contains the following: — MacDougal, Some Aspects of Desert Vegetation; Safford, Extracts from the Note-Book of a Naturalist on the Island of Guam — XII; Barrett, A Forgotten Fruit; and Waters, Field Notes.

Rhodora for October contains the following articles: — Robinson, Insecticides used at the Gray Herbarium; Fernald, A new Kobresia in the Aroostook Valley; Cushman, Notes on New England Desmids

— II; Wentworth, Two Plants new to the Flora of Lynn, Mass.; Woolson, New Station for *Asplenium ebeneum Hortonae*; B. M. Britton, A New England Station for *Buxbaumia indusiata*; Rand, Galinsoga in Maine; and A Leaflet of the Seal Harbor Village Improvement Society.

Part 3 of *Trees and Shrubs*, issued Nov. 14, adds still further to the number of American species of Crataegus.

The Bulletin of the Torrey Botanical Club for October contains the following articles: — Cannon, Studies in Plant Hybrids — The Spermatogenesis of Hybrid Peas; and Evans, Hepaticæ of Puerto Rico — III.

The Bryologist, for November, contains the following: — Britton, The Splachnums; Holzinger, On Some Fossil Mosses; Grant, Some Moss Societies; Miller, *Buxbaumia aphylla*; and Clarke, Mounting Mosses.

In addition to an important paper on Crassulaceæ, by Britton and Rose, vol. 3, no. 9, of the *Bulletin of the New York Botanical Garden* contains a paper by Berry on the Flora of the Matawan Formation, one by Williams on Bolivian Mosses, and one by Zeleny on the Dimensional Relations of the Members of Compound Leaves.

The *Bulletin of the Torrey Botanical Club*, for December, contains the following articles: — Griggs, On Some Species of Heliconia; Underwood, Summary of our Present Knowledge of the Ferns of the Philippines; and Kupfer, Anatomy and Physiology of *Baccharis genistelloides*.

The Fern Bulletin, for October, contains the following articles: — Gilbert, The Fern Flora of New York; Clute, Fernwort Notes — IV; House, Scolopendrium from Canada; Eaton, The Genus Equisetum in North America — XV; Clute, The Species-conception among the Ternate Botrychiums; and Druery, New Forms of Ferns. A portrait of Mr. Maxon forms the frontispiece to the number.

Part II of the botanical portion of the *International Catalogue of Scientific Literature* has been issued under date of November, 1903. It is of nearly double the size of the first part (626 pages), and is essentially on the same lines as the earlier part.

The *Journal of Mycology*, for October, contains the following articles: — Morgan, Some Western Specimens; Morgan, Note on *Corticium leucothrix*; I. Kellerman, The Accentuation of Mycological

Compound Names; Ellis and Everhart, New Species of Fungi from Various Localities; Kellerman, Minor Mycological Notes — I; Ohio Fungi, Fascicle VIII [descriptions and annotations]; Index to North American Mycology (continued); and Notes from Mycological Literature — VI.

The *Journal of the Royal Horticultural Society*, for October, contains a number of botanically interesting articles.

The fourteenth *Report of the Missouri Botanical Garden*, in addition to the customary administrative reports, contains a Supplementary Catalogue of the prelinnean library of the Garden, and a revision of the genus Lonicera, by Rehder.

Rhodora, for November, contains the following: — Ames, Hybrids in Spiranthes and Habenaria; Leavitt, Reversionary Stages in *Drosera intermedia*; Waters, *Asplenium ebenium proliferum*; Eaton, Notes on *Botrychium tenebrosum*; Deane, Gaylussacia in New Hampshire — a Correction; and Eaton, New Varieties of Isoetes.

Torreya, for October, contains the following: — Underwood, The Early Writers on Ferns and their Collections — 1, Linnæus; Howe, Note on the "Flowering" of the Lakes in the Adirondacks; and MacKenzie, A New Genus of North American Umbelliferæ [Pseudotænidia].

Torreya, for November, contains the following articles: Wooton, Ferns of the Organ Mountains; House, Notes on the Flora of Oneida Lake and Vicinity; Earle, Key to the North American Species of Inocybe — 1; Berry, A Question for Morphologists; Stone, *Arisæma pusillum* in Pennsylvania and New Jersey; and Nash, A New Bamboo from Cuba.

CORRESPONDENCE.

To the Editor of the American Naturalist:

SIR: — In a suggestive article in the *American Naturalist* for August (XXXVII, 551–555), on "Vernacular names of animals," Dr. Edwin W. Doran remarks, "I believe that I am the first who has thought it necessary to prepare a synonymy of the vernacular names of animals" and announces that "the author has in preparation a synonymy of all the vernacular names of vertebrates." It is evident from this, and from interviews had with other naturalists, that a great work on the subject published more than a century ago is unknown to most who are especially interested in its subject-matter. Indeed, I have found that none of the naturalists of Washington whom I had asked knew about it, so completely has it been forgotten. Nevertheless, it is a work in four large quarto volumes of about 2400 pages with 4783 numbered columns and some additional leaves (preliminary) as noted below. I give the title of the work and analysis of the volumes.

General title.

Allgemeines | Polyglotten-Lexicon | der | Naturgeschichte | von | Philip Andreas | Nemnich, J. U. L. | *mut. mut.* See below. | Zu finden | Hamburg, bey Licentiat Nemnich | [etc.]

The title page of the first part is printed from a plate; those of the other parts from regular type. They are paged for or were bound in four volumes as follows:—

I.

[Erste Lieferung. A—Canus.] Eng. title page + 8 p. l. + col. 1–840. 1793.

Zweyte Lieferung. | — | Cap. — Fus. | title page + col. 841–1684. 1793.

II.

Dritte Lieferung. | G—N. | title page + col. 1–740. 1794.
Virete Lieferung. | O—Z. | title page + col. 741–1592. 1795.

III.

Fünfte Lieferung. | — | 1) Deutsches Wörterbuch der Naturgeschichte. | 2) Englisches Wörterbuch der Naturgeschichte. | title page + col. 1–676 (= Fünfte Lief. Deutsches W.) + col. 677–1056 (= Sechste Lief.). [No date.]

IV.

Siebente Lieferung. | — | 1) Frazösisches Wörterbuch der Naturgeschichte | 2) Italienisches Wörterbuch der Naturgeschichte. | title page + col. 1057–1376 (= Französisches W.) + col. 1377–1507 (= Italienisches W.) [No date.]

Achte und letzte Lieferung. | — | 1) Spanisches Wörterbuch der Naturgeschichte. | 2) Holländisches Wörterbuch der Naturgeschichte. | 3) Schwedisches Wörterbuch der Naturgeschichte. | 4) Dänisches, Norwegisches und Islandisches Wörterbuch der Naturgeschichte. | 5) Einige Nachträge. | title page + col. 1509–2108. 1798.

This bibliographical description will suffice to give some idea of the nature and extent of the work. It is only necessary to add that in the first 2 volumes, under each Linnæan genus, alphabetically arranged, the species are enumerated under their Latin names in alphabetical order and the vernacular names in different languages added under the Latin ones. Thus, under *Anas boschas domestica*, as "*Engl*," 12 names applied to the subspecies as a whole in English as well as Gaelic, Welsh and Cornish, 3 of the drake, and 3 of the young are given; under *Anas boschas fera* 4 names are given as "*Engl.*"

It cannot be claimed that the English part is well done but the author at least "thought it necessary to prepare a synonymy of the vernacular names of animals" and carried the idea into execution in a very voluminous work.

Another noteworthy work carrying out the same idea for certain North American birds is Gurdon Trumbull's volume on "Names and Portraits of Birds which interest gunners," published in 1888.

Numerous minor contributions to the same subject have been published.

THEO. GILL.

(*No. 446 was mailed April 28, 1904*).

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THE ANATOMY OF THE NORTH AMERICAN CONIFERALES TOGETHER WITH CERTAIN EXOTIC SPECIES FROM JAPAN AND AUSTRALASIA. PART I.

D. P. PENHALLOW.

Introductory.

The present work had its origin in 1880, in an attempt to construct a system of classification for the North American Coniferæ, based upon the anatomy of the vascular cylinder of the mature stem. The fundamental idea was that such a classification would prove of great value in the identification of material used for structural purposes, but investigations had not been carried very far when it became manifest that some such arrangement was imperatively demanded in other directions and for purposes of a more strictly scientific character. In entering upon the study of fossil plants it was recognized that the most fruitful source of reliable data must be found in the stem structure. At that time there was little in the way of an adequate basis for further study of this sort, inasmuch as the current diagnoses of the vascular structure were found in most cases to be singularly inadequate, and often so incorrect as to require exten-

sive revisions. It was furthermore found that, in order to reach correct conclusions in the case of stems which must often present marked structural alterations arising through the influence of decay and other conditions attending fossilization in its various forms, it was indispensable that there should be a trustworthy means of comparison with existing types, whereby sources of error arising from eliminated structures might be definitely excluded, and the fossil referred with certainty to its nearest relative. The original intention was therefore modified with a view to meeting the requirements of palæobotanical research. During the twenty odd years these investigations have been in progress, there has been much change in the views held by botanists respecting the significance of anatomical features as affording evidence of descent, and our own studies brought forth facts which gave repeated emphasis of the most positive kind, to the idea that questions of phylogeny cannot be settled either by the morphologist in the narrower sense or the physiologist, either separately or combined, and that a proper historical point of view can be gained only when to such labors we join the data derived from a critical study of the stem structure in all its details. As the greater may always be held to include the less, the present discussion is to be regarded primarily from the biological point of view, and questions of descent will take precedence over those of mere taxonomy.

The original intention was to make a complete study of all the North American woods, comprising, as enumerated by Sargent in his report in the *Tenth Census of the United States*, some four hundred and nineteen species and varieties; but the great importance of the Coniferæ from an economic point of view, their frequent representation in the fossil state and their relatively more simple structure, eventually led to their selection as the one group in which initial studies might be prosecuted with the most immediate and profitable results. While the North American species constituted the original basis, various exotic species were added from time to time with the result that our studies as now completed, comprise ninety-two species from North America, twenty-one species from Japan, and four species from Australasia. This extension has proved of great value, not only from a

palæontological point of view, but also because of the important bearing such exotic types have had in the solution of questions relating to descent. The methods adopted in these investigations have already been fully explained (38, p. 33 *et seq.*) and further details at this time are uncalled for.

In 1896 the work had reached such a point that it was deemed desirable to make a preliminary statement of results. This appeared in a paper published in the *Transactions of the Royal Society of Canada* entitled the "Generic Characters of the North American Taxaceæ and Coniferæ," in which it was shown that generic differentiations were possible. The diagnoses and artificial key to the genera thus published, have been in constant use since that time for the determination of fossil species, with the most gratifying results; and after seven years of severe testing, and in the light of more extended studies, they are found to be substantially correct and reliable.

The question of specific differentiation presented a far more difficult problem, the solution of which has now been reached as embodied in the present work.

In the prosecution of these studies I have been under deep and often constant obligations to helpful friends working along other lines. To Prof. C. S. Sargent of the Arnold Arboretum, as also to Mr. Morris K. Jesup, President of the American Museum of Natural History; Dr. N. L. Britton, Director of the New York Botanical Gardens; the late Baron Ferd. von Mueller of Melbourne, Australia; Sir W. T. Thistleton-Dyer, Director of the Royal Gardens, Kew; and to Mr. E. J. Maxwell of Montreal I am indebted for much valuable type material. To Dr. B. E. Fernow, formerly Chief of the Bureau of Forestry of the United States Department of Agriculture, I am under obligations for a large amount of material specially selected with reference to testing the accuracy of diagnoses and details of the key. To Mr. J. G. Jack of the Arnold Arboretum, I am under particular obligations for the readiness with which he has frequently responded to requests for material of a trustworthy character, and his care in selecting a large series of specimens for testing purposes, which have contributed very largely to the success of the final results. To my assistant,

Miss C. M. Derick, I wish to extend my appreciation of the frequent and valuable assistance she has rendered.

Spiral Tracheids.

In the genesis of the vascular system, the elements first differentiated from the generative tissue, constitute the primitive elements now generally recognized in accordance with the designation of Russow as protoxylem. These elements are tracheids, and in the Coniferales as also in the Ginkgoales, they always occupy a position immediately external to the pith and therefore on the inner face of the zone representing the growth of the first year, but they are not repeated in the formation of xylem structure in subsequent years. The primitive character of such tracheids is therefore indicated, not only by their position and relation to development of other parts, but it is also exhibited by their occurrence in plants where the vascular system is of a far more simplified type and of which they constitute relatively more prominent features. In the Equisetineæ, both fossil and recent, they are conspicuous elements of the vascular structure, being found within the limits of the carinal canal. They similarly occur in the Ophioglossaceæ and elsewhere among the more primitive of the vascular plants. The general evidence, then, which may be derived from a comparative study of various types, tends to enforce the idea that, originating as a primitive form of the wood structure, and more or less common to all the vascular plants, they are relatively predominant in the lower forms, with a tendency to obliteration through replacement or modification in the higher types, where their presence may be held to represent a survival of ancestral characters. This view gains additional support from a study of the peculiar structural variations which characterize such tracheids, and the progressive modifications which they have been found to undergo in relation to the development of the secondary xylem.

The protoxylem elements are distinguished by the presence of thin, spiral bands disposed upon the inner surface of the primary wall in such a manner as to afford a substantial measure of mechanical support. These ribbon-like bands represent second-

ary growth in thickness of a local nature — the localization being determined with reference to the requirements of such support in the first instance. De Bary (9, p. 57) has shown that they exhibit considerable variety in the number of fibres and the direction and steepness of the coils. Their number is often only 1–2 in narrow tubes which are first formed when the differentiation of tissues begins, in others 4 or more, and it rises in many cases in the angiosperms to 16–20. He has furthermore pointed out that the steepness of the coils is greatest in those tubes which are developed earliest, before the extension of the part to which they belong has ceased; since in these the coils are separated from one another by the extension which the tube itself undergoes. These facts appear to suggest that the more typical the spiral tracheid is, the more fully does it emphasize the idea of a primitive structure; but that as the spirals become more dense or closer, there is a tendency toward more uniform and less localized secondary growth of the wall, as expressed in the structure of the higher types of plants or the secondary xylem elements of the Coniferæ. In confirmation of such a view, reference may be made to the commonly observed fact that the spirals tend to a more compact arrangement at the ends of the elements, becoming correspondingly more open in the central region; and likewise to the well known transitional forms which these structures exhibit, whereby their original characteristics are completely lost as they merge ultimately into tracheids devoid of spirals, but characterized by the presence of pits of various forms. In 1840, Don (52) pointed out that the tracheids of *Cycas revoluta* exhibit scalariform structure at one end and bordered pits at the other. This fact has more recently been commented upon by Williamson who observed the same fact independently, and drew from it the inference that a definite relation exists between the scalariform markings and the pit structures of such a nature that the one is the natural successor of the other. In *Ginkgo biloba* which is now generally conceded to represent a much more primitive type than the Coniferæ, though more advanced than the cycads, precisely similar transformations are to be met with. The evidence of fossil plants is quite as convincing as that derived from existing

FIG. 1.

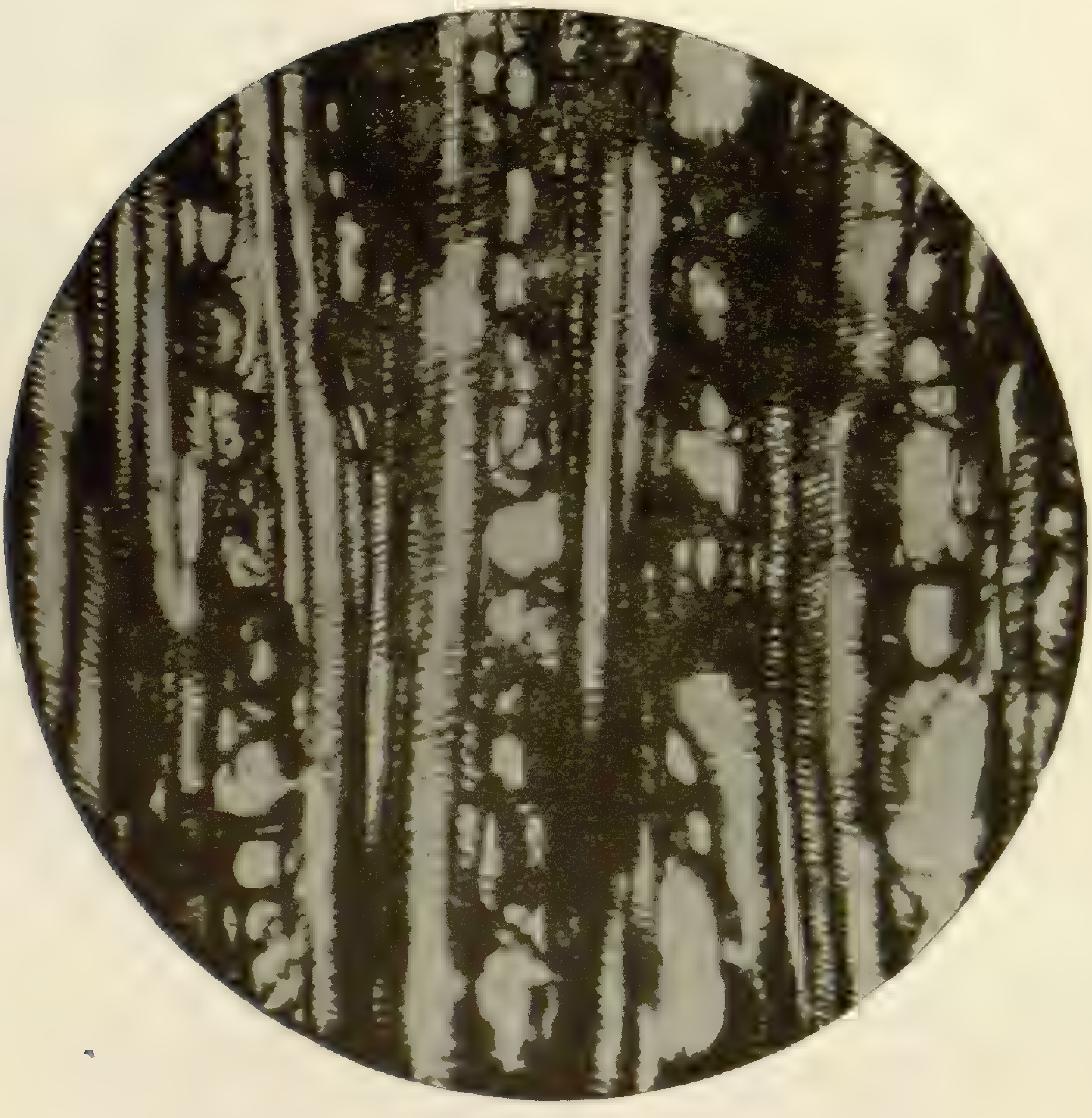

FIG. 2.

FIG. 3.

FIG. 4.

FIGS. 1–4.—*Cordaited brandlingii.* Radial series showing the origin of bordered pits from spiral tracheids. × 180.

species, while it is often of distinctly greater value because affording data derived from presumably more primitive types. Thus such transitions are well known, though of a relatively simplified form in the structure of the calamitean stem, and an excellent example of this kind is afforded by a figure given by Scott (43, p. 22). In 1869 Williamson (52, p. 69) directed attention to the occurrence of such transformations in the tracheids of Cordaites (Dadoxylon). A more recent study of this genus (39, p. 57 and 43, p. 418) has shown that this feature is well exhibited in *C. brandlingii*, where a suitable radial section (Figs. 1–4) will present a more or less graduated series of transitions from the typical spiral tracheid of the protoxylem, through scalariform structures to the multiseriate bordered pits of the tracheids in the secondary xylem; while within the limits of the same tracheid, such transitions may be observed as it were, in process of development, affording the most conclusive proof in this respect. These transitions as observed in *Cordaites brandlingii* show the following phases:

In the successive radial development of new tracheids, there is a constant tendency to a more uniform thickening of the cell wall by secondary growth. This at first finds expression in the more compact arrangement of the spirals which later coalesce at various points, thus giving rise to more localized areas devoid of secondary growth, and hence to a scalariform structure in which the general lines conform more or less exactly, to the direction of the original spirals. By a further modification the elongated, thin areas become converted into shorter, often isodiametric areas substantially by a process of division. A further tendency to general thickening of the walls causes the margins of the scalariform structure to project from all sides and extend over the area of arrested growth as a lip which never completely closes at the centre, where there is left a usually circular, sometimes oval or again lenticular or even oblong opening, and in this manner the bordered pit is formed.

The region within which these changes occur, or the "transition zone," is subject to great variation whereby the change from spiral to bordered pit may arise very gradually through a broad radial zone, as in *Cordaites brandlingii* or it may occur very

abruptly as in the modern Coniferæ. The general tendency of such evidence is to show that with a higher type of organization, there is a corresponding diminution in the transition zone and increased abruptness in the structural alterations. The logical result of an extension of this process would be the reduction of the bordered pit to the condition of a simple pit, and ultimately, its complete obliteration. In ~~the~~ Coniferæ the reduction of the bordered pit to the condition of a simple pit sometimes occurs in the case of medullary rays or even in the case of tracheids with very thick walls, but it becomes most prominent in the angiosperms where it is a characteristic feature. Instances also occur in some of the hard pines, in which the pit is completely obliterated. This applies in particular to tracheids of the summer wood, the walls of which have become unusually thickened.

The relations to which attention has thus been directed somewhat in detail, have been expressed in more general terms by De Bary (9, p. 321) in the statement that "Outside the primitive elements, wider trachæ follow. Their development takes place successively, advancing from the inner edge of the bundle outwards, and as a rule at a time when the elongation of the entire part to which they belong is nearly at an end. The thickenings on their walls therefore have a successively denser arrangement: dense spiral and annular trachæ, then reticulated and pitted trachæ follow one another in succession from within outwards, with gradual transitions, or with the omission of one or the other immediate form." It is probably a justifiable inference from the preceding facts that, the relation which exists between the spiral tracheids of the protoxylem and the pitted tracheids of the secondary xylem in the Coniferæ, is, in general terms and from the standpoint of development, the same as that exhibited between the lower and higher types of vascular plants.

Accepting the general principle which appears to be justified by the foregoing facts, that the transition from spirals to bordered pits is a feature in development which bears a direct relation to the evolution of higher types of organization, we may utilize it for the purpose of determining the general phylogeny of the Coniferæ so far as they may show a survival of such characters. Out of a total of 117 investigated species of indigenous

and exotic Coniferæ, 9.4 % show a more or less permanent survival of the spiral structure within the limits of the secondary xylem. Of these 6 % fall within the Taxaceæ (Torreya 3.45 %, Taxus 2.5 %), while in the Coniferæ the remainder is divided between Pseudotsuga (1.7 %), Larix (0.86 %) and Pinus (0.86 %). In the genus Torreya the spirals are, on the whole, rather open and distinguished by being 2–4 seriate. They are typical throughout the spring wood, but in the thin summer wood they quickly become vestigial and ultimately disappear altogether. In *T. taxifolia* there is also a marked condensation whereby the spirals are all brought into a more compact series within the earlier tracheids of the summer wood. All of these changes appear to be directly related to a progressive increase in the thickness of the tracheid wall.

In all investigated species of Torreya, there is a rather wide variation in the angle which the spirals make with the axis of growth, and this becomes most pronounced in *T. californica*, which gives the lowest angle for any species of either Torreya or Taxus. Usually the spiral has an angle quite distinct from that of the lines of striation in the cell wall, but in *T. taxifolia* the two often coincide. The following will show the various details derived from the average of ten measurements for each species.

	Average angle.	Highest angle.	Lowest angle.	Extreme range.
Torreya nucifera	70.5	87.0	57.0	30.0
" *taxifolia*	70.4	77.0	61.0	16.0
" *californica*	46.2	63.0	30.0	33.0
Means	62.3	75.7	49.3	26.3

In the genus Taxus, the spirals are rather close and in 2, rarely 3 series. As in Torreya they are typical throughout the spring wood, and show a pronounced tendency to obliteration in the summer wood. This tendency is subject to considerable variation in different species. In *T. canadensis* the spirals are conspicuous throughout. In *T. floridana* they usually disappear

in the later growth and are wholly wanting in the two or three, last formed tracheids. In *T. brevifolia* they become very imperfect in the outer summer wood and tend to disappear completely, only vestiges remaining in the last formed tracheids. In *T. cuspidata* the spirals are generally absent from the summer wood, or when present, they are merely vestigial. The angle is somewhat greater — about 7 deg.— than in Torreya, and this fact is apparent with respect to certain species without special measurement. The four species appear to be paired off in such a way as to represent a mean difference of about 10.9 deg. as between *T. canadensis* and *T. floridana* on the one hand, *T. brevifolia* and *T. cuspidata* on the other. In all cases the angles of the spirals are quite distinct from those of the lines of striation. The following details are based upon the average of ten determinations.

	Average angle.	Highest angle.	Lowest angle.	Extreme range.	Mean of 2
Taxus canadensis . . .	72.4	88.0	66.0	22.0	
" *floridana* . . .	78.4	90.0	72.0	18.0	75.4
" *brevifolia* . . .	63.0	76.0	55.0	21.0	
" *cuspidata* . . .	66.1	87.0	45.0	42.0	64.5
Means . . .	69.9	85.2	59.5	25.7	

A comparison of these results in detail emphasizes the fact that the distribution of the spirals, as between spring and summer wood, is in direct harmony with the principles already stated, and furthermore, that the angles at which the spirals develop do not afford an adequate basis for generic differentiation. It is nevertheless possible to recognize sub-generic groups in such wise that in both genera a general line of division may be established at 70 degrees. In the case of *Torreya californica*, the very low angle of 46.2 degrees may be regarded as a differential character of specific value.

In the genus Pseudotsuga, spirals are confined to the tracheids of the spring wood. This has a partial exception in *P. macrocarpa*, in which vestigial spirals may be observed in the earlier tracheids of the summer wood. In this species the mean

angle is 70 degrees, but the spirals are always characterized by lack of prominence, they are often widely distant, and the somewhat extended areas within which they are wholly wanting or fragmentary, suggests a process of obliteration. In *P. douglassi* the average angle is 82 degrees; the spirals are characterized by considerable prominence and they are also, on the whole, close. In this genus these two factors obviously possess a well defined differential value with respect to the two species.

Among the higher genera only two cases are known in which spirals occur, but in each the character is of a very sporadic nature. In *Larix americana* spirals are frequently found in the summer wood, but they are so inconstant in their occurrence, and they present such varying aspects, that the angle cannot be determined. In *Pinus tæda*, where the walls of the summer tracheids are very thick, rudiments of spirals may sometimes be seen. Here also it is manifestly impossible to determine the angle.

Viewing these five genera collectively, their spirals conform fully, in their occurrence and relation to progressive development, to the general principles already stated, and especially as formulated by De Bary. They possess no differential value of generic rank with respect to Pinus and Larix, but they do have such value with respect to Torreya and Taxus on the one hand, and Pseudotsuga on the other, the differentiation resting upon their occurrence in the summer wood in the former, and their exclusion from that region in the latter. Were any question to arise in this connection, it could be authoritatively decided by the definite association of resin passages and fusiform rays in Pseudotsuga.

It only remains for us to ascertain how far such structural features may be employed as a basis upon which to determine the general phylogeny of the genera. As between Torreya and Taxus there is very little upon which to base conclusions respecting sequence in development, and it is apparent that both of these genera have attained to nearly the same level. Such differences as do exist, however, seem to point to the relatively, though slightly, inferior position of Torreya as indicated by (1) the smaller angle in that genus and (2) the generally more com-

pact spirals of Taxus. This fact, so far as it possesses phylogenetic value, appears to confirm the conclusions as to the relative positions of these two genera, already determined upon the basis of external morphology as stated by Eichler (11, p. 108).

It has already been made clear from the preceding facts, as well as from former discussions (40, p. 56) that in the case of the Taxaceæ and also of Pseudotsuga, the spirals must be regarded as a survival of primitive structures. On a former occasion (40, p. 57) I was inclined to consider that their occurrence in Larix and *Pinus tæda* was atavistic, but in the light of more recent evidence as now set forth, this opinion requires modification in so far as to include the idea that they do not express mere parallelisms in development, but that they afford evidence of a common ancestral type at some point far anterior to the evolution of the Taxaceæ. We must therefore consider that Torreya, Taxus, Pseudotsuga, Larix and Pinus represent different branches of a general phylum — undoubtedly including also, other closely related genera in which the spirals have been wholly obliterated — which had its origin at a point anterior even to such types as Cordaites, and therefore, in all probability in what Coulter (7) has very happily designated as "the great Cordaitean plexus" arising from the eusporangiate ferns, or what, according to our more recent knowledge, and Coulter's more recently expressed view (8, p. 172) would be designated as the Cycadofilices.

Bordered Pits Distribution and Structure.

In the preceding pages, the derivation of the bordered pit from the spiral tracheid, and its obviously more intimate relation to a higher type of development have been made clear. Our present purpose is to discuss these structures with special reference to (1) occurrence, (2) distribution, (3) structural modifications, (4) taxonomic value and (5) their value as evidences of descent.

At the outset, reference may be made to the occurrence of bordered pits on the radial walls of the ray cells as exhibited typically in Sequoia and Taxodium. Their location in such situa-

tions, as also upon the radial, terminal, upper and lower walls of the ray tracheids may be held to represent a feature somewhat distinct from their presence on the walls of the wood tracheids, and their consideration properly belongs to a discussion of the medullary ray as a whole; but it may be observed that they constitute a characteristic feature in the structure of the ray elements in the great majority of the Coniferales.

The occurrence of bordered pits on the walls — especially the radial walls — of the wood tracheids in the Ginkgoales and Coniferales, is much too familiar a fact to call for special discussion at this time, but reference may be made to the additional fact that their characteristic structure is such as to permit of their use for the general purpose of tracing possible lines of descent through such extinct types as Cordaites and the Cycadifilices. It is true that similar bordered pits originating in modifications of spiral structures, are to be met with, often in great numbers, in the higher angiosperms, but in such cases the associated structures permit of a clear and definite differentiation of all such woods from the Coniferales.

Radial walls.— The characteristic situation of the bordered pits is on the radial walls where, as was shown many years since by De Bary (9, p. 160), "the pits of contiguous tracheids always correspond to one another in such a way that on each limiting surface, all the cavities of the pits of one fit exactly over those of the other. The plano-convex cavities are thus applied to one another in pairs so as to form the lens-shaped pit cavities" as seen in tangential section. But on surfaces abutting on elements of another order, *e. g.*, parenchyma cells, the bordered pits of the tracheids correspond to non-bordered pits, or they are opposite an unpitted wall. Four typical variations of the bordered pits may be recognized: — (1) the multiseriate, when they are disposed in any number of rows more than two, (2) the 2-seriate, (3) the uni-seriate with occasional pairs of pits, and (4) the strictly uni-seriate. The general sequence thus presented will be found to be in direct accord with the evolution of higher types of structure and organization.

The most primitive type of gymnosperm presenting a multiseriate arrangement, is the genus Cordaites. Among eleven

species of this genus which have been critically studied within recent years (39) there is a general agreement in the constancy of this character which thereby becomes of generic value. In all the species the pits are disposed in such a compact manner throughout the entire extent of the tracheid, as to present a hexagonal outline. In *Cordaites acadianum*, they are 2–5-seriate (Fig. 5). In other species they vary from 2-seriate in *C. hamiltonense* and *C. newberryi* (Fig. 6) to occasionally 4-seriate in *C. clarkei*. In the majority of species, the rows are not constant, but show a varying number from 1 to 3, or 2 to 5, this variation

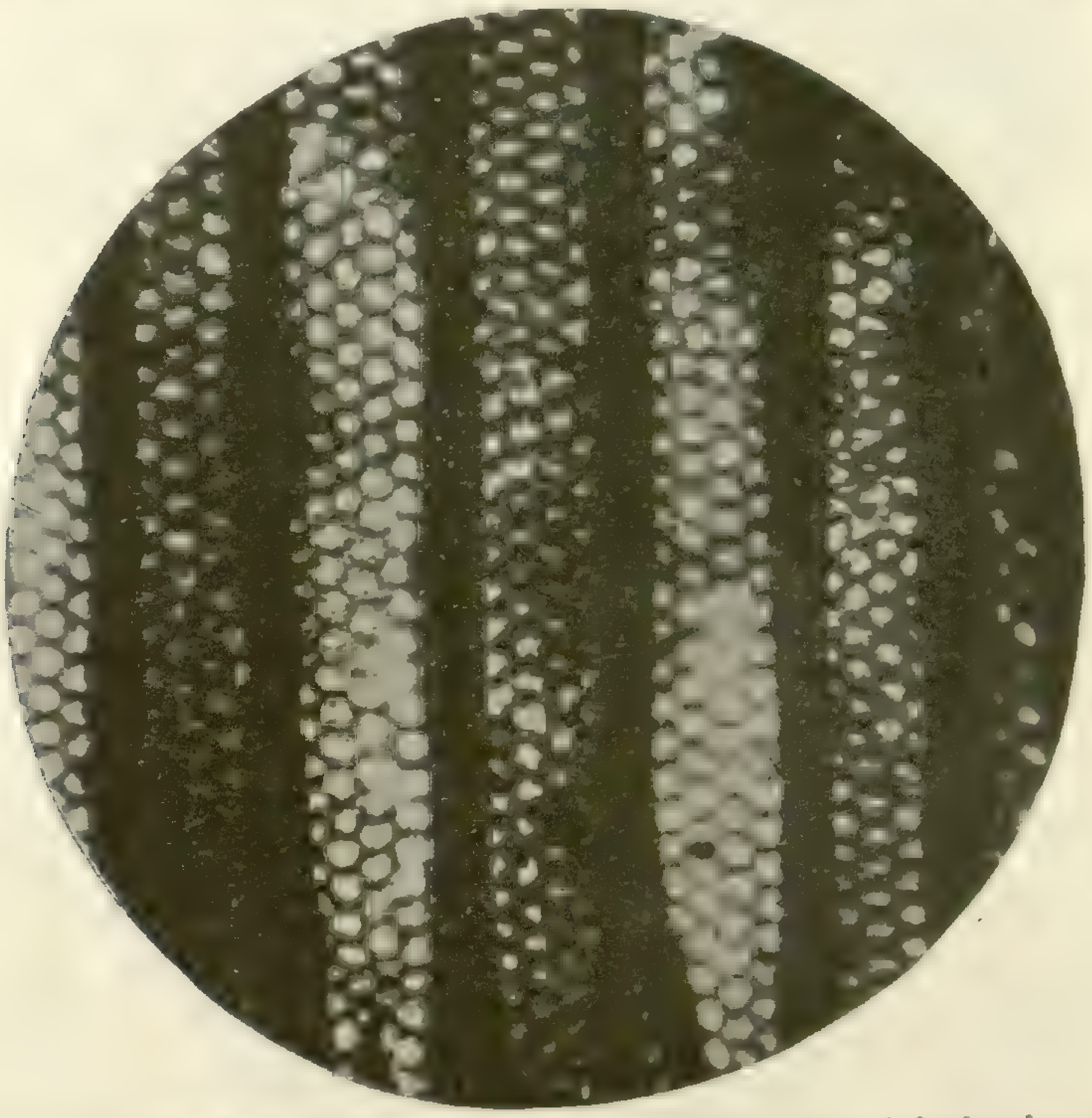

FIG. 5.— *Cordaites acadianum*. Radial section showing disposition of the bordered pits. × 180.

being exhibited by adjacent tracheids in accordance with the variation of the latter in radial diameter; and viewing this distribution as a whole, it cannot be doubted that it represents corresponding differences in development. One of the most striking features of the genus is to be met with in *C. newberryi* (Fig. 6), which is unique in the segregation of the pits into groups of 6–13.

In Araucarioxylon Knowlton has shown (25, p. 614) that, while conforming to the characteristic form and compact arrangement presented in Cordaites, the pits exhibit far less constancy in their serial arrangement, and in this respect they are at once

comparable with those of the existing Araucarias. Among the latter, *A. cunninghamii* shows a 1–3-seriate disposition; *A. excelsa* is 1–2-seriate while *A. bidwillii* is strictly 1-seriate. All

Fig. 6.— *Cordaites newberryi.* Radial section showing disposition of the bordered pits. × 180.

of the extinct species as comprised in the genus Araucarioxylon not only show similar variations, but such variations are found to cover a much wider range. A comparison of all the species, both recent and extinct, now available for that purpose, is of interest in this connection.

	1-ser.	2-ser.	3-ser.	4-ser.
A. bidwillii	x			
wurtembergianum	x			
schmidianum	x			
hugelianum	x			
excelsa		x		
arizonicum		x		
edwardianum		x		
virginianum		x		
doeringii		x		
subtile		x		
argilliacola			x	
heerii			x	
cunninghamii			x	
robertianum				x

Such a comparison brings into strong relief the fact that the Araucarias, both past and present, constitute a transitional group with a somewhat wide range of variations, and in this respect they may be said to stand between the more stable Cordaites and Agathis on the one hand, and the far more variable Coniferæ on the other, since in *Agathis australis* we find essentially the same features of structure and distribution as in Cord-

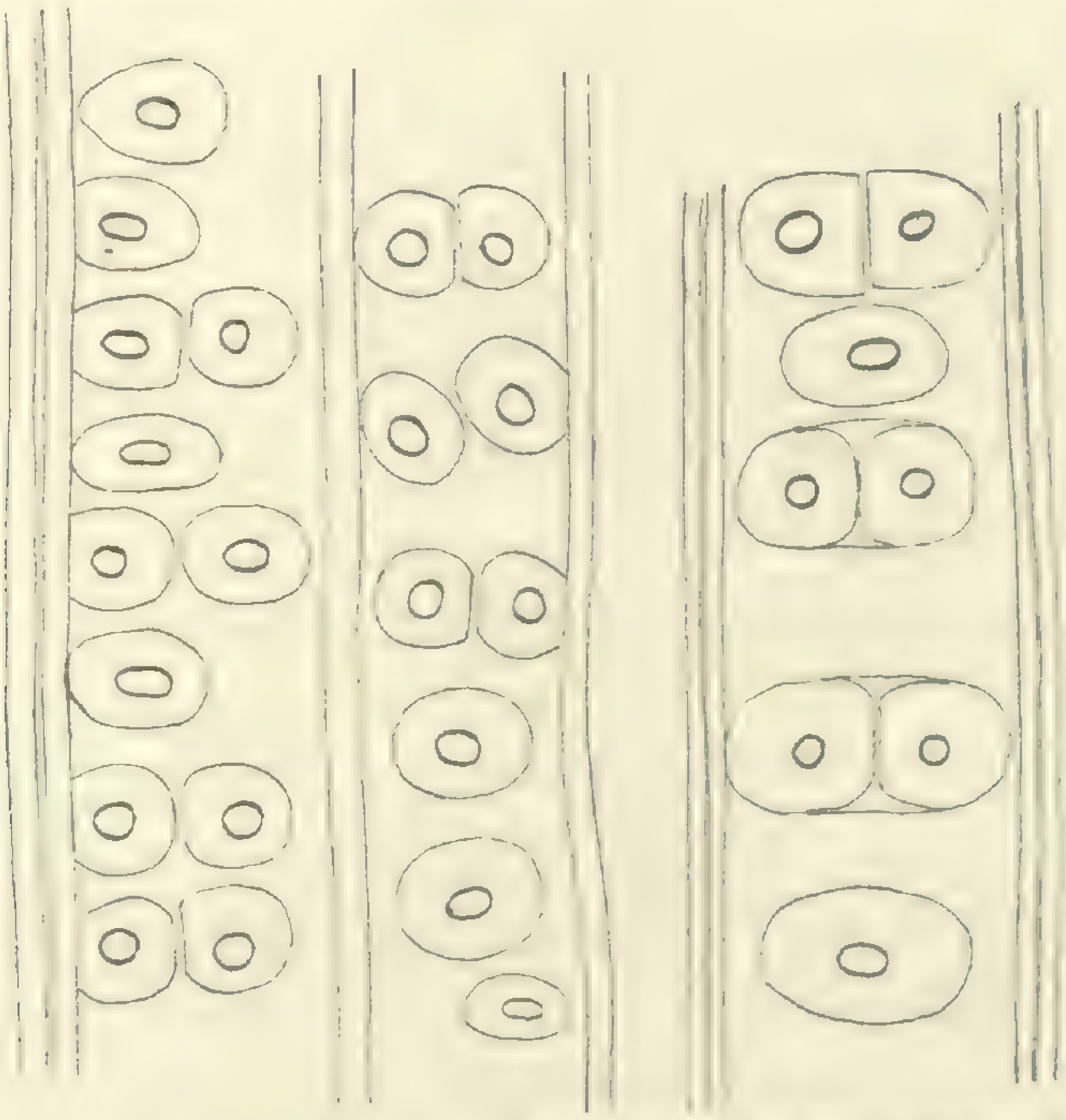

FIG. 7.—*Pinus cubensis.* Radial section showing the form and disposition of the bordered pits. × 280.

aites, the pits being 1–3-seriate. The sequence presented above may be held to be in the inverse order of development, and *A. robertianum* must therefore be held to represent the most primitive form.

It is apparent that in Cordaites, Araucaria (including Araucarioxylon) and Agathis, the pits are invariably distinguished by two constant features; (1) their hexagonal form and (2) their very compact disposition throughout the entire extent of the tracheid. They often deviate from the multiseriate arrangement typical of the group as a whole, in that in individual cases they are reduced to a 1-seriate arrangement. They thus tend to overlap the next group which is distinguished by a 2-seriate disposition, but any confusion which might arise from this cause, may be overcome by reference to the special form and dis-

position of the pits as will more fully appear in the following lines.

Among the remaining Coniferales, 20 species of various genera, or 17.2 % in all, show a 2-seriate arrangement, and to this group we must also add the Ginkgoales and various fossil species. Here the multiseriate disposition of the pits involves features which at once distinguish the group as a whole from the preceding, clearly placing it upon a higher plane of development. The pits are never hexagonal but generally elliptical or round, while they also show a strong tendency to extreme segregation. When brought into a compact arrangement as in Cupressoxylon, Sequoia or various species of Pinus, they are flattened only along the lines of limited contact, which are usually confined to one end (Fig. 7). A very characteristic feature of this group is the further fact that the 2-seriate arrangement is not constant, either in the same section or in the same tracheid. Both *Pinus tæda* and *P. cubensis*, as also *Larix americana* and *Tsuga canadensis* afford illustrations that while typically 2-seriate, a given section may show a strictly 1-seriate arrangement, and this difference also obtains as between contiguous cells. In all such cases examination will show that the variation is directly related to the relative size of the tracheids in such a way that the narrower tracheids, or those arising from a less vigorous growth, are 1-seriate. Within the individual tracheid there is a strong tendency to a 1-seriate arrangement in the central region, while it is 2-seriate at the extremities; and this law holds so true that in those species which are exceptionally 2-seriate, judgment should be reserved until it is seen that the 1-seriate form holds throughout.

The antithesis of the multiseriate type is found in the 1-serite form. This is typical of 50 % of all the species included in the present studies. In such cases the form of the pit is never hexagonal or specially flattened. When the disposition is somewhat compact, as in *Pinus strobus* (Fig. 8), the outline becomes more or less strongly elliptical, but as the segregation is more pronounced, a definitely circular form prevails (Fig. 9). Within the limits of the individual tracheid the same law of distribution obtains as in the 2-seriate type, whereby segregation is always most pronounced in the central region.

Between species of the strictly 1-seriate, and those of the strictly 2-seriate type, there is an intermediate or transition group comprising 34 species, or 29.3 % of the investigated species, into which members of the first two groups may occasionally be projected. The distinguishing feature of this group is the occurrence of pits in pairs which are usually distant, and in no case so numerous as to distinguish a 2-seriate disposition. They give undoubted proof of the passage from one type to the other. Like the 2-seriate type, this feature is not confined to any one genus or to any particular group of genera, but it applies with equal force to any genus, the members of which may therefore represent any or all of the three types here specified.

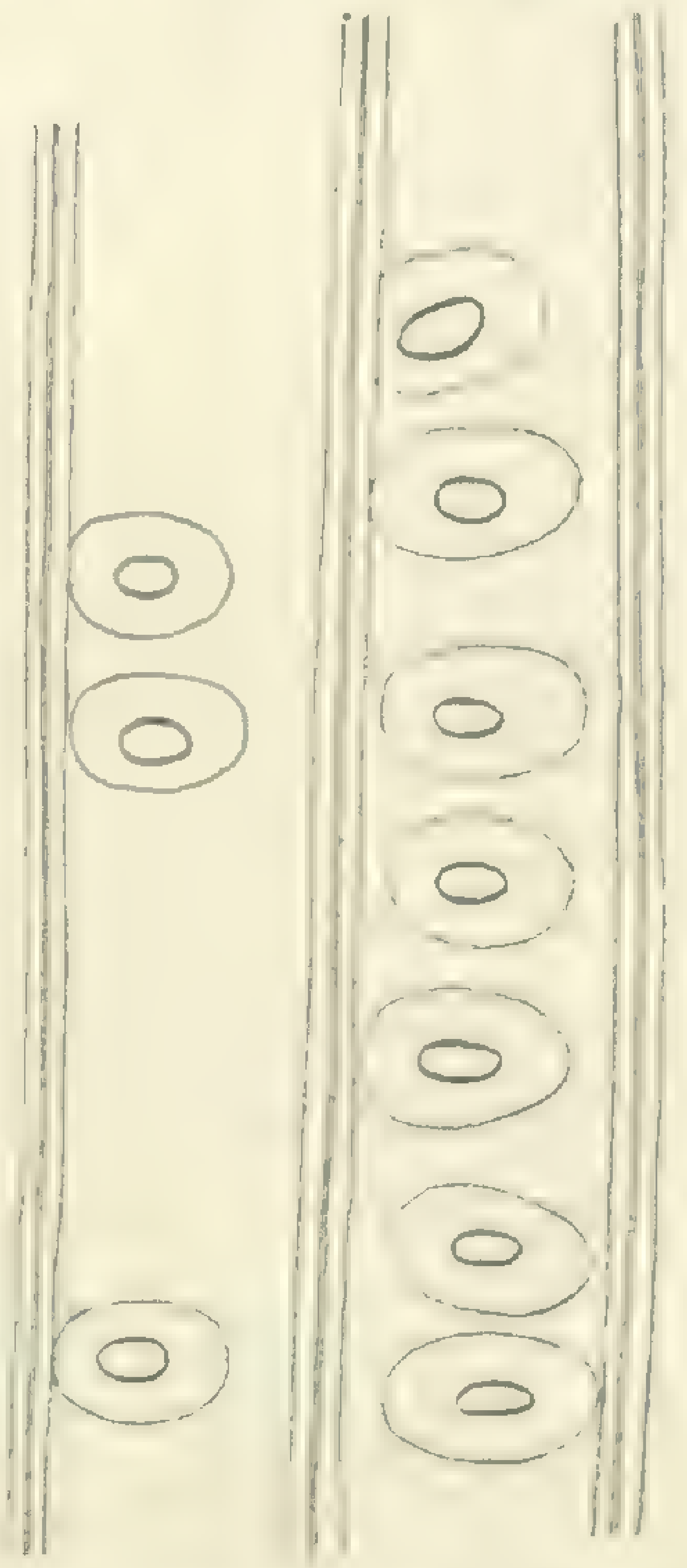

Fig. 8.—*Pinus strobus*. Radial section showing the form and disposition of the bordered pits. × 280.

Viewing the distribution of the bordered pits from the standpoint of zonal development, it is found to be universally true that, in the earlier spring wood there is the strongest tendency to a multiseriate arrangement. With a radial increase of the xylem, this tendency constantly diminishes, with the general result that the pits become more strictly uniseriate and more distant toward the summer wood in which they are sometimes wholly obliterated — this being the case when the cell wall acquires unusual thickness.

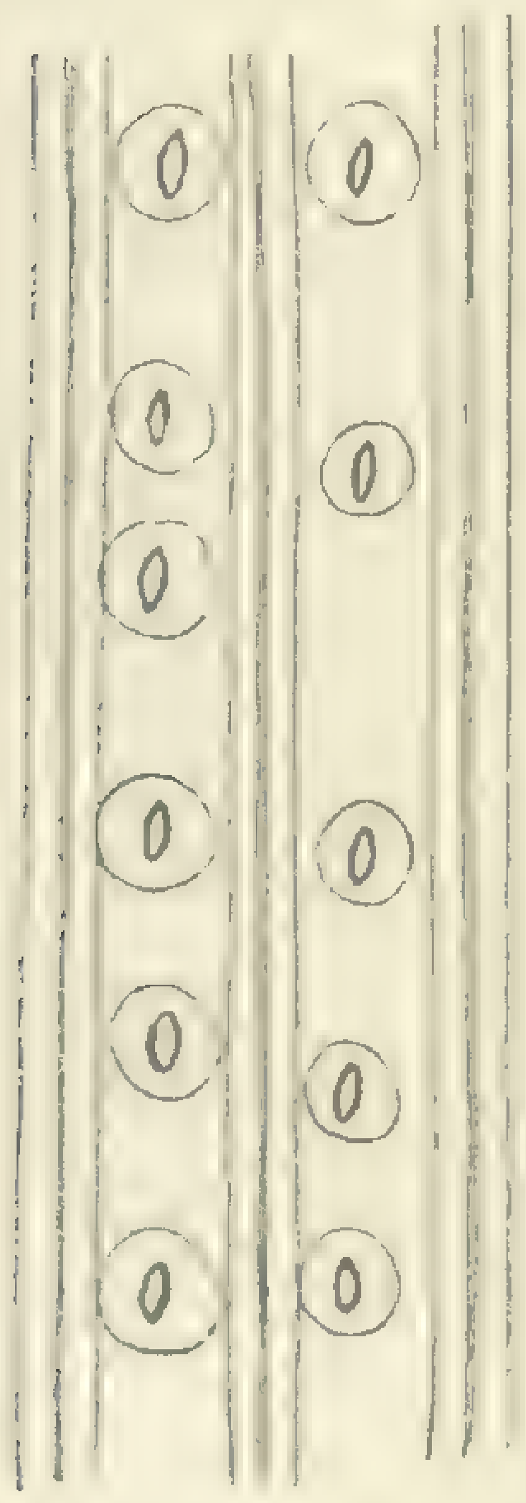

Fig. 9.—*Pinus strobus*. Radial section showing the bordered pits of the summer wood. × 280.

Upon careful examination, the foregoing facts will be found to be in exact accord with the law formulated by De Bary with reference to variations in the structure of spiral tracheids and the genesis of bordered pits as already stated. In accordance with this law it is possible to conclude that relatively rapid growth is coördinated with a primitive development, while the converse

is true of a slow rate of growth which is again convertible into terms of maturity. On this basis we may present the following general outline of sequence in development, as preliminary to further and more detailed discussion of phylogeny.

Cordaites.	2–5 seriate,	hexagonal pits.	Compact throughout the tracheid.
Araucarioxylon.	1–4 "	" "	
Araucaria.	1–3 "	" "	
Agathis.	1–3 "	" "	
Ginkgo.	1–2 "	round or oval pits.	More or less, often strongly segregated.
Higher Coniferales.	1–2 "	" " " "	
" "	1–ser. & pairs	" " " "	
" "	1–seriate.	" " " "	

Tangential Walls. — The occurrence of bordered pits on the tangential walls is a well-known and characteristic feature of the Coniferales. In the case of fossil forms, to which Araucarioxylon offers a partial exception, it cannot be satisfactorially demonstrated because of the peculiar alterations of the cell wall, but that it is present we are permitted to infer from analogy with existing species upon which dependence must be placed for an elucidation of the general law. The typical position for such pits is upon the tangential walls of the summer wood, where they are most satisfactorily seen in radial section, inasmuch as they are always readily observable when present, and their most essential features are displayed in a manner not possible in a tangential section (Fig. 10). Pits occur in this position in 71.7 % of all the investigated species, and their absence in 28.3 % points to some special features in development which may be assumed to have a general bearing upon the question of descent and relationship. In Agathis, as represented by the one species, *A. australis*, such pits are a prominent and characteristic feature, but in the nearly related Araucaria, they are remarkable for their uniform absence. In the primitive Ginkgoales they

Fig. 10 — *Sequoia gigantea.* Radial section showing the bordered pits on the tangential walls of the summer wood. × 280.

are also present, but among the Taxaceæ, while generally present, they are occasionally wanting as in *Torreya taxifolia* and *T. nucifera* or 66.6 % of the investigated species of that genus. Nowhere else among the Coniferales do we find such a feature until we reach the genus Pinus, the second and higher section of which is invariably characterized by their absence, thus presenting an exceptional feature to the extent of 68.3 % of that genus. That such absence represents a process of obliteration conformable to De Bary's law cannot be doubted, while the sporadic recurrence of this feature in often widely separated genera, or in particular species of a given genus, must be held to have a more or less direct bearing upon the general course of development. This is emphasized by the observation that in *Larix americana* and *L. leptolepis* as also in *Picea bicolor*, there is a more or less pronounced tendency to an obliteration which is never fully developed. This is expressed in the somewhat remote position of the pits and their very small size, which renders them obscure and often difficult to discover. In this respect these species represent transitional forms.

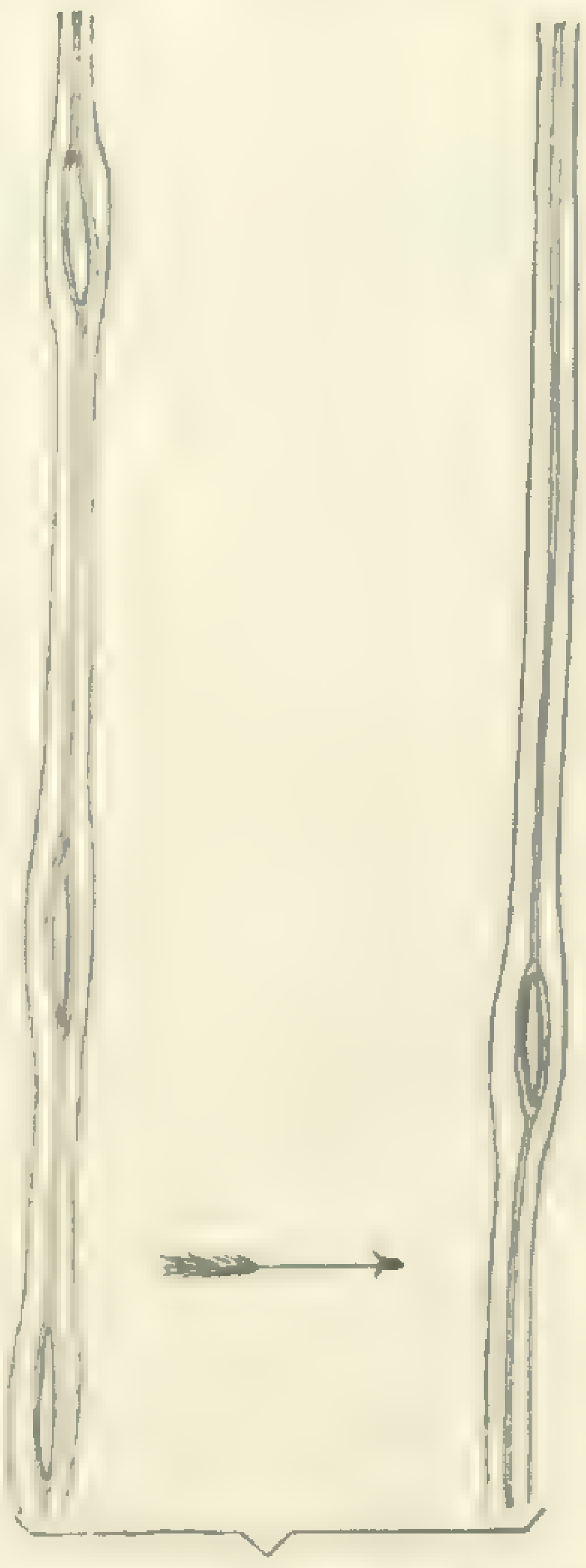

Fig. 11.—*Sequoia gigantea.* Radial section showing the bordered pits on the tangential walls of the spring wood. × 280.

As an exceptional feature, bordered pits may sometimes be found upon the tangential walls of the spring wood. This is especially noticeable at the ends of tracheids, and in rare cases it may apply to the entire extent of the wall. The most notable instance of this kind, because practically unique, is to be met with in *Sequoia gigantea* (Figs.

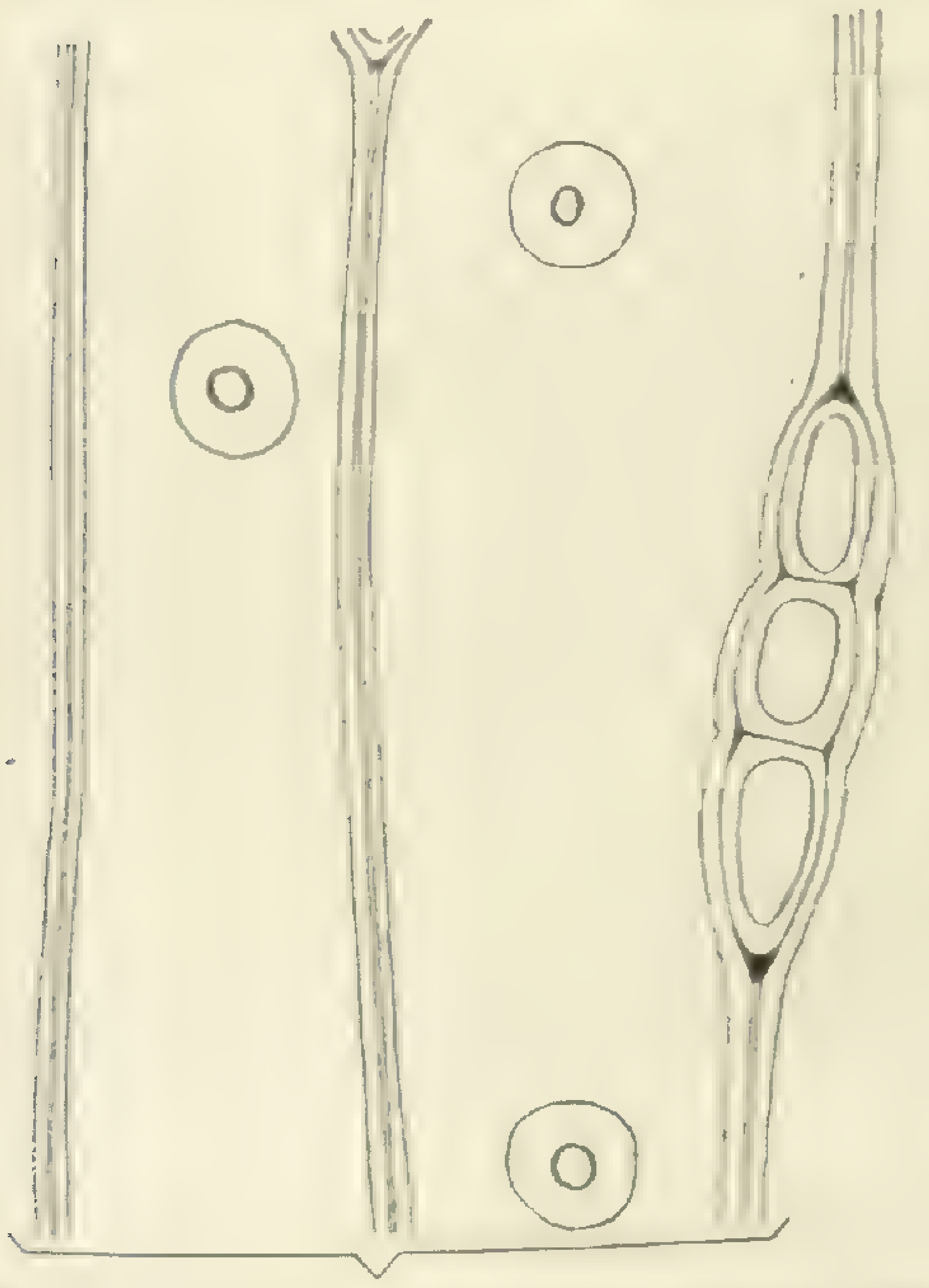

Fig. 12.—*Sequoia gigantea.* Radial section showing bordered pits on the tangential walls of the spring wood. × 280.

11, 12). Those spring tracheids which lie in direct contact with the summer wood of the previous year, often exhibit this feature with great prominence, but it may also extend radially through several successive tracheids. This is undoubtedly a primitive character, and in the one case cited it possesses some value for the purpose of specific differentiation, but in general terms, the occurrence of bordered pits in such positions is of so sporadic a nature as to give this feature no well defined value, either for taxonomic or phylogenetic purposes. It may, nevertheless, be stated with respect to the pits on the tangential walls of the tracheids in general, that in their distribution they distinctly conform to the law governing similar structures on the radial walls.

Reference to *Cordaites acadianum* shows that in the multiseriate pits of the hexagonal form, these structures always preserve the spiral arrangement characteristic of the structures from which they were derived (Fig. 4), and this conformity also extends to the direction of the spirals which generally ascend from left to right. The general law in this respect has already been formulated so fully by De Bary (9, p. 163), as to make it unnecessary at this time to enter upon its consideration more in detail, beyond a reference to one or two special features and some apparently exceptional cases. While the spiral arrangement is always typical in such genera as Cordaites, Agathis, Araucaria, etc., it is not obvious in those cases where the pits are strictly uniseriate and often remote from one another. Nor is it apparent at first sight in those cases of 2-seriate pits where, as in *Cupressoxylon dawsoni* from the Cretaceous, *Larix americana*, Sequoia and various species of Pinus, the pits are always paired off in such a way that the axis of each pair is at right angles to the axis of the cell (Fig. 7). Two explanations are here possible: (1) the spirals are in reality 2-seriate, and they are projected through the alternate members of the two rows of pits, or (2) the disposition of the pits represents an extreme phase in the flattening of the original spirals conformably to a higher type of development. This latter view, which seems the more reasonable, is in direct harmony with De Bary's law, while it receives additional support from the form and direction of the pit orifice.

The orifice of the pit is variable, at different times being round, when the pits are also round and more or less distant; oval or oblong, when the pits assume corresponding forms; or in the summer wood, lenticular or oblong. The transversely elliptical pits of *Pinus strobus* (Fig. 8), the orifice of which is also transversely oblong, as also the similar pits of Pinus cubensis (Fig. 7), afford substantial proof in confirmation of the probable correctness of this view. In the summer wood, the pit orifice commonly assumes a position which appears to offer a direct contradiction of this conclusion. In *Pinus strobus* (Fig. 9), the orifice is oblong and parallel with the tracheid axis. In *Pinus pungens*, as in many others of the same genus (Fig. 13), the narrow orifice is extended above and below into a diagonal slit of great length, forming a narrow angle with the tracheid axis. At first sight this would seem to imply that these features represent primitive spirals, the original direction of which has not been greatly if at all modified, but one or two considerations will assist us to a correct interpretation of this feature. In the first place it is to be observed that such positions and modifications of the orifice are invariably associated with the summer wood, or where they occur in the spring wood, it is the result of maceration and commonly occurs in fossil plants, or woods in process of decay, and they are always most conspicuous in those tracheids which have experienced the most profound modifications with respect to the growth in thickness of the secondary walls. It has already been shown in the case of Taxus and Torreya, that there is no necessary connection between the spiral bands and the spiral lines of striation — that, as a matter of fact, as particularly illustrated by *Torreya taxifolia*, the two are quite distinct from one another under ordinary conditions of development. But in cases where the wall experiences extreme growth in thickness, the obliteration of the original spiral structure is complete, and at the same time it is replaced by the normal striation of the wall which,

FIG. 13.—*Pinus pungens*. Bordered pits on the radial walls of the summer wood. × 280.

in such cases becomes most pronounced. Instances such as those afforded by *Pinus strobus* and *P. insignis* may, according to this interpretation, be held to represent the final phases in the obliteration of the original spirals, and they therefore constitute characters indicative of the highest type of development. In a few cases the structure of the bordered pit presents exceptional forms. In *Cupressus nootkatensis* the pit orifice shows either unusual want of regularity in outline and marked eccentricity of position, or it is so enlarged as to leave only a narrow border to the round or oval pit (Fig. 14). Similar features occur occasionally in other genera, and they are generally conspicuous in *Pinus tæda*. De Bary (9, p. 159) has directed attention to the same feature in Ephedra and *Pinus sylvestris*, and he correctly interprets it as a form of arrested development. Alterations also arise as a feature of secondary growth in those cases in which the wall acquires unusual thickness. This is typically the case in *Pinus cubensis* where in plan (Fig. 15), the orifice is extended vertically to a length often twice the diameter of the original pit. In tangential section, according to the particular direction of the plane of section (Fig. 16), the orifice is either of uniform width, or it enlarges constantly through the entire thickness of the later growth, from within outwards. That such unusual forms are features of extreme, secondary growth of the wall, and that they may be anticipated in all cases where such modifications of the walls occur, is a reasonable deduction from the observed facts.

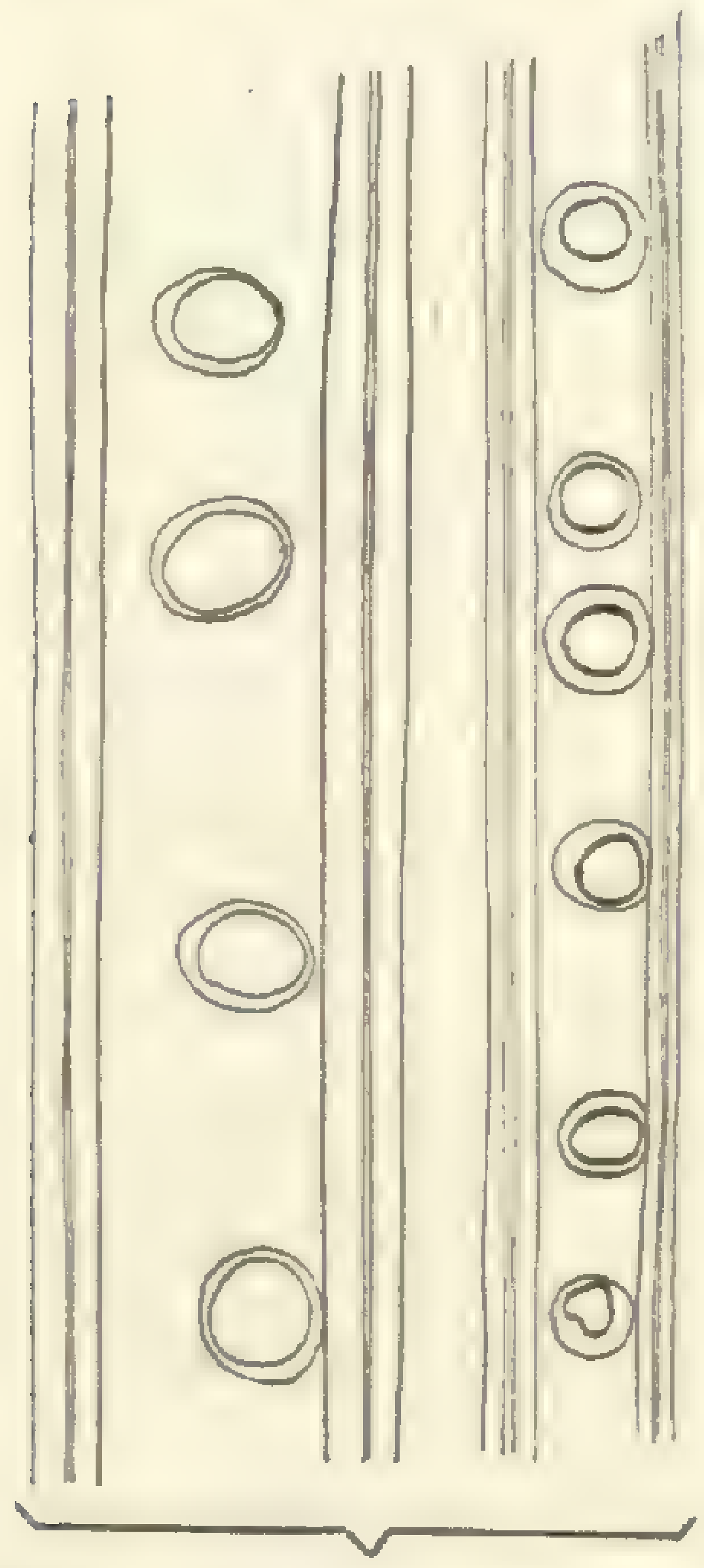

FIG. 14.—*Cupressus nootkatensis.* Radial section showing deformed bordered pits. × 280.

FIG. 15.—*Pinus cubensis.* Radial section showing deformed bordered pits. × 280.

FIG. 16.—*Pinus cubensis.* Tangential section of bordered pits as in Fig. 15. × 280.

Taxonomic and Phylogenetic.

For taxonomic purposes, the bordered pits possess a definite though often limited value. In the genus Cordaites, as also in Araucarioxylon, Araucaria and Agathis, this is expressed in the hexagonal form together with their very compact, chiefly multiseriate arrangement throughout the entire extent of the tracheids, — characters which are of generic value and at once serve to separate these genera from all others. The contrasting differential feature is then to be found in the pits of the oval or round form, together with their 2-seriate or 1-seriate disposition with a more or less marked tendency to segregation. This is characteristic of the Ginkgoales and all the Coniferales, both fossil and recent.

As a different character of sub-generic value, the occurrence of bordered pits on the tangential walls of the summer wood of the first section of Pines — the soft pines — and their invariable absence from the same structural region in the second section — the hard pines, — is one which may be always relied upon.

For the purposes of specific differentiations, the pits on the tangential walls possess a distinctly inferior value which must be confirmed in most cases by the evidence of other factors. Their utility in this respect is made sufficiently clear in the various diagnoses and in the artificial key, without further discussion at this time.[1]

In the genus Cordaites, according to the provisional specific differentiations of fossil forms as at present generally employed, the number of rows of pits, or their segregation into definite groups, are characters of well defined, specific value, since they are among the few features which may be utilized with certainty for this purpose. Thus *C. acadianum* with its 2–5 rows; *C. materiarium* with 2–4 rarely 3–4 rows; *C. hamiltonense* with two rows and *C. newberryi* with two rows in groups of 6–13 pits, rest upon a basis which is not only easy of recognition, but which may be applied with full assurance, as has been done

[1] This paper will appear in the *Trans. Royal Society of Canada* for 1904.

on former occasions (38, p. 51 et seq.) In Araucaria, the three species investigated may be similarly differentiated from one another. The same rule is applicable to *Torreya taxifolia* which is thereby separable from the other species ; likewise to *Cupressoxylon dawsoni*, *Tsuga canadensis*, *Larix americana*, and, among the pines, *P. lambertiana*, *P. clausa*, *P. sabiniana*, *P. tæda*, *P. palustris*, and *P. cubensis*. It is to be observed, however, that the constancy which characterizes this feature in Cordaites and Araucaria, is wanting in the higher Abietineæ. In Larix there is such variation that very careful scrutiny is required, while in the genus Pinus, the number of exceptions to the typical character increases greatly, and is liable to cause some difficulty in the final determinations unless much care is exercised. *Pinus tæda* offers a conspicuous illustration of this fact, as may be seen by reference to the analytical key. It is therefore manifest that the value of the bordered pits for taxonomic purposes is most clearly defined in the lower types of the Coniferales, and that their value diminishes steadily, with an advance toward higher forms of organization and development. In all cases where exceptional forms introduce diagnostic difficulties, these may be overcome by the controlling effect of associated characters.

We are now in a position to examime the data at hand with a view to determining the bearing of the bordered pits upon questions of phylogeny.

Having reference to the origin of the bordered pit and the various modifications it presents in the course of development, it cannot be doubted that the hexagonal, multiseriate pits of Cordaites, Araucarioxylon, Araucaria and Agathis place those genera in a relatively inferior position, a view which gains a large measure of support from the well known and extensively multiseriate disposition shown in *Heterangium grievii* (49, p. 341), but the facts so far discussed have not as yet thrown any special light upon the relative positions of the separate genera.

An examination of twelve species of Cordaites shows that the bordered pits exhibit a much wider range of serial variation than any other genus covered by the present studies. If then we accept the general principle with respect to the development of the bordered pits as already illustrated, it cannot be doubted that

the 2–5-seriate pits stand much nearer to the primitive form of the tracheid than do the 1-seriate. From this point of view it is then evident that in *C. recentium*, the name of which is thereby seen to be fully justified, the 1-seriate pits place it at the upper end of a series which has its inferior termination in the 2–5-seriate *C. acadianum*, while between the two, intermediate forms appear as members of a series of nine variants, and it is possible to arrange these in such a manner as to exhibit the probable sequence in development as follows:—

Serial variations in the Bordered Pits of Cordaites.

	2–5 ser.	3–4 rarely 2.	2–4 chiefly 3.	3–4 chiefly 2.	2–3 rarely 4.	2–3 chiefly 2.	1–3 chiefly 2	2-ser.	1-ser.
C. acadianum	x								
ohioense		x							
ouangondianus			x						
materiarium				x					
clarkii					x				
annulatum						x			
brandlingii							x		
materioide							x		
illinoisense							x		
hamiltonense								x	
newberryi								x	
recentium									x

The wide range of variations here shown, especially when compared with other genera, at once serves to suggest that Cordaites was in this respect somewhat of the nature of a transition group from which others were given off, or else that it epitomized the collective changes through which a number of genera must have passed. And inasmuch as this genus exhibits a more highly developed, multiseriate arrangement than any other within the general phylum, we must concede that it is, with respect to this character, the most primitive of all.

The genus Araucaria shows a much more restricted range of variations, there being only four variants pretty uniformly distributed among fourteen species, both recent and fossil. While the most highly developed members, four in number, are represented by 1-seriate pits, the most primitive form of 4-seri-

ate pits occurs in only one case — *A. robertianum*. It is therefore manifest that this genus is obviously of a more advanced type than Cordaites from which it undoubtedly originated. Agathis being represented by only one species, it is not possible to locate it more definitely than to say that the 1–3-seriate disposition of its pits would place it in a position equivalent to that occupied by *Araucaria cunninghami* and therefore about three-fourths way down the scale for that genus. This fact points with much force to the idea that of the two genera, Agathis is of relatively lower type.

The Ginkgoales and the Coniferales as a whole, exhibit an obviously higher type of development than the preceding group, in consequence of the more pronounced tendency to segregation of the pits which are now either elliptical or round, and never hexagonal. This distinction is so clearly defined and constant as to support the idea which gains force in other ways, that Cordaites, Araucaria and Agathis are clearly related members of a principal branch of the original stock, and that they therefore diverge considerably from the particular line of descent within which we find both the Ginkgoales and the Coniferales.

The observations so far made apply altogether to the pits on the radial walls. We may now pass to a consideration of their relation to the tangential walls, a factor which does not call for very extended discussion. This feature is found to apply to 71.7 % of all investigated species exclusive of fossils. It is wanting in three species of Araucaria, representing 2.58 %; in Torreya, 2 species or 1.72 %, and in the entire second section of Pinus to the extent of 28 species or 24.1 %. But the occurrence of pits on the tangential walls, in common with those on the radial walls, is a well known feature of the Sigillarias (49, p. 198), where their primitive character is well established, and we can hardly doubt that their ultimate elimination in the higher pines is the expression of a final phase in development, consistent with the position usually assigned those plants. The absence of pits from the tangential walls of certain Araucarias and Torreyas, is to be interpreted as one of those sporadic tendencies toward a higher type of development which never become permanent in the same line, but which are to be met with as one of the invariable features of evolution.

Ginkgo, being the unique representative of an ancient line, cannot very well be brought into the present discussion very much in detail. On other grounds it is known to be a primitive form representing a group distinctly inferior to the Coniferales, and this view is supported by the disposition of the pits in two series, a character which, if taken alone, would give the genus rank with *Torreya taxifolia* among the Taxaceæ, but when regarded collectively, would place the genus distinctly below the Coniferales as a whole. This evidence, then, indicates that the Ginkgoales must have arisen as a side line at some point inferior to the Coniferales, but superior to the Cordaitales.

In the Taxaceæ the bordered pits do not in themselves afford very conclusive evidence as to the relative position of the family. Among the eight investigated species, representative of three genera, only three, and chiefly two variants occur. Taken alone, the disposition of the pits would lead to no final conclusion, but other factors permit of placing this family in the inferior position usually assigned to it. Within the genus three variants are found — the 1–2 rows of *T. taxifolia*, the one row or pairs of *T. californica* and the strictly 1-seriate form of *T. nucifera*. In Taxus only two variants appear — the one row or pairs of *T. floridana* and the 1-seriate disposition as found in the remaining three species. The one representative of Podocarpus shows but one variant, and that is 1-seriate. From this it is obvious that the generic sequence must be in the order given, and that the sequence of species must be approximately as given in the table of anatomical data to follow.[1]

The remaining genera of the Coniferales present so few deviations from a typical form, that they cannot be differentiated fully on the basis of the bordered pits. This character nevertheless has a definite value in association with others, as in the genus Sequoia or some of the hard pines, *Larix americana*, etc. The general sequence of genera may be recognized by the bordered pits only in so far as these structures serve to confirm and emphasize the conclusions reached in other ways, and this will become apparent from an inspection of the table of anatom-

[1] This table will appear in the last number of this series.

ical data. It will nevertheless serve a useful purpose at the present moment, to ascertain the general sequence based upon the percentage distribution of the principal variants as follows.

Comparison of the principal variations in the serial arrangement of bordered pits, by percentages.

	Total var.	2–5	2–4	2–3	1–3	2	1–2	1+ pairs.	1
Cordaites . .	9	8.3	25.0	16.6	25.0	16.6			8.3
Agathis . . .	1		6.6	20.0			40.0		33.3
Araucaria . .	4		6.6	20.0			40.0		33.3
Ginkgo . . .	1						100.0		
Sequoia . . .	1						100.0		
Larix . . .	3						33.3	33.3	33.3
Taxodium . .	2						25.0		75.0
Libocedrus . .	1							100.0	
Thuya . . .	1							100.0	
Pseudotsuga .	2							50.0	50.0
Pinus . . .	3						17.1	41.5	41.4
Abies . . .	3						13.6	27.3	59.1
Taxus . . .	2							25.0	75.0
Tsuga . . .	3						16.7	16.7	66.6
Picea . . .	2							10.0	90.0
Podocarpus .	1								100.0
Thujopsis . .	1								100.0
Cryptomeria .	1								100.0

With respect to specific differentiations, it has already appeared that the bordered pits may be employed with success in Taxus and Torreya. In Cupressus this rule also applies to *C. pisifera*, and *C. macrocarpa*, both of which are distinguished by having their pits in one row or pairs, while the remaining seven species have strictly uniseriate pits. An instructive example is afforded by *Cupressoxylon dawsoni.* In this species, which is of early Tertiary age (Lignite Tertiary), the pits are typically 2-seriate, being disposed in a very compact manner similar to that found in existing Sequoias. But in a series of eleven specimens, it is clearly seen that two variants are represented — the second being a 1-seriate form. These variations are also found, as in the other Coniferales, to be directly related to variations in the size and rate of growth of the tracheid. It cannot be doubted then, that *C. dawsoni* is a more primitive representative

than any species now existing, and that it is substantially the ancestral form of the genus, so far as we know.

In Larix the four investigated species may be differentiated pretty fully, and this rule applies with particular force to *L. americana*, and *L. occidentalis*, both of which are distinguished by a 2-seriate form. Among the pines, *P. lambertiana*, *P. clausa*, *P. sabiniana*, *P. tæda*, *P. palustris*, and *P. cubensis* are readily differentiated from the others by the 2-seriate pits. In all other cases than those specifically indicated, the bordered pits afford an inadequate basis for specific differentiation.

It is now apparent that segregated, round or oval pits in one row must be taken as representing the highest type of development in the Coniferales, and any deviation from this must be taken to indicate the survival of more primitive conditions, pointing to derivation from a type like that of Araucaria or Cordaites. From this point of view, the occurrence of pits in 1–2 rows in *Larix americana*, *Torreya taxifolia*, Sequoia, *Tanga canadensis* and various species of Pinus, indicates the survival of ancestral characters which are partial to the extent of 7.2 %, and complete to the extent of 10.8 %. That such deviations from the usual type of structure are either survivals or reversions which serve to indicate a common origin, cannot be doubted, more especially as they do not occur at a fixed point near the original type, but they arise sporadically in widely separated genera. The tendency of such evidence then, is to show a common ancestry for the various genera of the Taxaceæ and Coniferæ, a view which is greatly strengthened by the testimony afforded by the spiral tracheids of *Larix americana*, Pseudotsuga and *Pinus tæda*. The provisional conclusions which we now reach are, that there were probably four main lines of descent from the original stock represented by Cordaites:

1 Araucaria and Agathis.

2 Ginkgoales.

3 Taxaceæ.

4 Coniferæ.

(*To be continued.*)

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. E. L. MARK, DIRECTOR.—No. 151.

THE SENSE OF HEARING IN THE GOLDFISH CARASSIUS AURATUS L.

HENRY B. BIGELOW.

I. INTRODUCTION.

TO THE older investigators, such as Hunter (:82) Müller ('48), and Owen ('66), the presence of internal ears in fishes was sufficient evidence that these animals had a sense of hearing. Kreidl ('95), however, was the first to seek experimental evidence on this point. He tested normal goldfishes, and others from which he had removed the semicircular canals with the attached portions of the ears. Since both classes of fishes reacted similarly to sounds, he concluded that the skin, not the ear, is stimulated by sound, and that, therefore, it can be said that goldfishes do not hear. This conclusion has since gained considerable recognition, and has been accepted by Mulertt (:02) in his recent book *The Goldfish*. Kreidl ('96) also made observations on the trout in the fish basins of the Benedictine Monastery at Krems, Austria, and gathered ample evidence to prove that the belief that the fish assembled for food at the ringing of a bell to be unfounded. These observations confirmed him in the opinion that fishes do not hear, a conclusion further supported by the subsequent observations of Lee ('98) on other species, particularly the dogfish.

In spite of this important evidence, Lang (:03) concludes a popular discussion of the question "Do acquatic animals hear?" with the statement that fishes and other like forms should be tested more extensively before a decisive answer can be given. Tullberg (:03), whose experiments led him to conclude that the fish ear receives stimuli from currents in the surrounding water,

admits the possibility that the ear may also be in some degree an organ of hearing. The fact that certain fishes do respond to what are beyond question sound vibrations in water was demonstrated independently by Zenneck (:03) for three fresh-water species, *Leuciscus rutilus*, *L. dobula*, and *Alburnus lucidus*, and by Parker (:03[a], :03[b]) for a salt-water species, *Fundulus heteroclitus*. Parker further showed that this response was dependent on the presence of a functional internal ear, and that, therefore, this species could be said to hear. But he could not get any response to sound from the smooth dogfish, and so was led to conclude that different fishes might differ widely in this respect, some possessing, some lacking, a true sense of hearing. Since none of the recent investigators who favor the view that fishes hear, have tested the species which, in Kreidl's hands, yielded negative results, it seemed desirable, in the light of recent work, to examine the goldfish again; and this I have undertaken to do. This problem was suggested to me by Professor G. H. Parker, and I am indebted to him for help, suggestions, and criticism throughout the series of experiments.

II. Methods.

In determining whether or not a fish has a sense of hearing it must be borne in mind that the responses to sound may be very slight and easily confused with responses to other stimuli; and, further, that, although the absence of response does not necessarily mean absence of hearing, the consistent occurrence of a response is fair evidence of the presence of this sense. To test normal goldfishes satisfactorily, it was necessary to isolate them from all other disturbances and to apply the sounding instrument as directly as possible to the water, but without causing any gross mechanical vibration. The apparatus which I used was an aquarium, some 30 cm. wide, 35 cm. long, and 15 cm. deep. The two sides were of glass, and the ends and bottom of clear white pine. The aquarium was placed on a wooden table which stood with its feet on many thicknesses of soft paper, thus isolating it from vibrations which might otherwise reach it through the floor. The bottom of the aquarium was covered on

the inside with a thick layer of cotton wool, which, in turn, was held in place by a sheet of thin cotton cloth to form a deadened floor. On trial, I found that the light entering through the glass sides of the aquarium was a source of disturbance to the fishes. Hence I later made these sides opaque by a covering of dark paper. My method of producing sound was by an electric tuning fork, which was run by a small storage battery and had a pitch of 100 vibrations per second. This was set up on another table, very close to the first one, but not in contact with it. The foot of this table also stood on many thicknesses of soft paper. The fork itself rested on a deadened support, and was so arranged that after it had been set in vibration, it could readily be moved till its base came in contact with the wooden end of the aquarium. This could easily be accomplished without observable jar to the water in the aquarium, and certainly in itself had no effect on the fishes. For when I made the fork, not in vibration, touch the aquarium in the usual way, the fishes gave no reaction, although to the vibrating fork they were very responsive; I tried this many times.

With this apparatus, I tested three classes of goldfishes; (1) normal ones; (2) fishes the greater part of whose integument had been made insensitive by cutting the fifth and seventh nerves, the lateral line nerves, and the spinal cord close to the medulla; and (3) fishes in which the eighth nerves had been cut.

III. Normal Fishes.

Goldfishes appear to be much more irregular in their responses to sound than some other fishes. When one is first placed in the aquarium, it swims about vigorously, darting from side to side in a very restless fashion. This extreme excitability lasts for a considerable time, often an hour; but finally the fish becomes more quiet, sinks to the bottom, and remains nearly motionless except for an almost incessant movement of the pectoral fins. In a few cases, the fishes lay motionless with these fins folded closely to their sides. If now the tuning fork was set in vibration, and brought into contact with the wooden

end of the aquarium, the fishes almost always responded by one of a number of reactions. The most important of these were: a rapid vibration of the tail without locomotion; sudden jerks of the tail from side to side, often so vigorous as to cause a swift dart forward; normal locomotion, forward, backward, or to one side; or in those fishes which lay at rest with the pectoral fins folded, a vigorous spreading of the pectorals. It was evident that individual goldfishes differed from one another in their reactions much more than the individuals of Fundulus as recorded by Parker (:03[a], p. 51). When a fish was tested with the vibrating fork, it might respond by any one of these reactions, but every fish had one distinct reaction characteristic of it, which the application of the fork rarely failed to elicit. Thus, the more active fishes usually responded by vigorous locomotion, the more quiescent ones, by tail or fin movements. Although fishes on which no operation had been performed, usually responded to the sound, one, an albino, and a very sluggish individual, gave no response. The fact that this one died soon after my observations on it were made, is perhaps an explanation of its unusual condition. As an example of the characters of the responses, the following record of ten tests from my laboratory note-book may serve. This record relates to a fish which was subsequently operated upon by cutting the eighth nerves.

1. Tail-jerks, followed by forward swimming.
2. Tail-jerks, then forward swimming after an interval of half a second.
3. Sudden tail- and trunk-jerks, followed by forward swimming.
4. Tail-jerks, but without locomotion.
5. Tail-vibration, but without locomotion.
6. Strong tail-vibration followed by a turn to one side.
7. Tail- and trunk-jerks, followed by forward swimming.
8. Tail-vibration, followed by a sudden turn to one side.
9. Tail- and trunk-jerks, followed by a turn to one side.
10. Tail-jerks, and sudden jump forward.

In all, I made 193 tests on 18 normal fishes, and observed 150 responses, about 78% of the whole. Of the 43 failures, to

respond, 12 were in the case of the albino fish above mentioned, and many of the remaining 31 were probably due to faulty observations caused by the extreme activity of the fishes. In this respect, there is a great difference between different individuals, some being in such continual movement that it is difficult to test them, while others are more generally quiet.

IV. Fishes with Insensitive Skins.

The second class of fishes tested were those in which the greater part of the skin had been rendered insensitive by cutting the spinal cord just posterior to the pectoral fins, as well as both lateral branches of the tenth, and the fifth and seventh nerves on both sides of the body. The fifth and seventh nerves were cut at a point just above the dorsal end of the opercular opening, where they come close to the skin. The fishes were etherized before the operation, and usually recovered and lived many weeks. The individuals selected for this operation were those which showed good pectoral-fin reactions when tested with the tuning fork. Such fishes after recovery lay on their sides on the cloth bottom of the aquarium, and were perfectly quiet unless stimulated. That their skins were practically insensitive was shown by the fact that they were quite indifferent to touch with a bristle or the like.

In 65 tests on 6 such fishes, I observed 52 responses (80%) to the vibrating fork, a condition essentially the same as that of normal fishes. These experiments demonstrate then, that with an almost insensitive skin, a goldfish will respond to sound as a normal fish does.

V. Fishes with Insensitive Ears.

The third class of fishes tested were those in which the eighth nerves had been cut on both sides. In preparing for this operation a number of fishes were tested and only such as showed a clear reaction to sound were operated on. They were etherized, and their eighth nerves were cut by piercing the skull in an appropriate position and cutting downward with a small chisel-

like knife. The chief danger in this operation is in cutting too deep, in which case excessive bleeding may follow. When this was avoided, the fishes usually recovered, and the success of the operation could be judged by their subsequent movements. When they first recovered from the ether they seemed to have lost all power of equilibration, swimming now one side up, and now the other, or resting with their long axes vertical. After about a day, however, they usually acquired and kept their normal position, at least while resting or swimming slowly ; and this ability increases, until after two or three weeks they were, in all their ordinary movements, indistinguishable from normal fishes. If, however, such a fish be placed in a large body of open water and made to swim rapidly, it soon loses all power of orientation and darts about, turning over and over until exhausted. This condition, so far as I know, is permanent, for in the case of one fish which lived for over three months after the operation these reactions showed no tendency to disappear, but persisted till death. The partial recovery of equilibrium noticeable soon after the operation is probably due to a successful attempt on the part of the fish to retain its normal position through sight.

Earless fishes are usually more quiet than normal ones, and hence they can very easily be tested. In all, I made 73 tests on 7 fishes, and in no instance did I get an undoubted response to sound. This is in strong contrast with the reactions of the same fishes before their eighth nerves had been cut, and points beyond question to the ear as an organ of hearing.

I supplemented the foregoing experiments by another series in which two normal fishes that I found to respond well to sound, were etherized, and the eighth nerve of each cut on the right side. After an interval of twenty-four hours, they were both tested again, and found to respond about as well as they did before the operation. In 20 tests on the two, there were 19 responses. They were then etherized again, and the eighth nerves of the left sides were cut. After recovery, they were tested once more, and, although the experiments were conducted with the greatest possible care, not a single response was observed in 20 trials. This experiment shows that the

operation of cutting the eighth nerve, severe as it is, is not sufficiently so to account for even a small part of the reduction in the number of responses which follows the elimination of both ears as sense organs.

In another instance, a fish which before any operation responded vigorously to sound by movements of the pectoral fins, was prepared by cutting two holes in the top of the skull, through which the eighth nerves could conveniently be reached, and the following parts were severed: the spinal cord, the lateral line branches of the tenth nerves, and the superficial portions of the fifth and seventh nerves of both sides. After recovery, the fish gave ten vigorous pectoral fin responses to as many trials with the sounding apparatus. The eighth nerves were then cut, and in twelve tests only one response, and that of a doubtful character, was observed. It, therefore, seems incredible that nervous shock can account for the almost complete loss of response to sound, after cutting the eighth nerves, and I am firmly convinced from the foregoing experiments, that the ear in the goldfish is an organ of hearing, and that it is the loss of this which is accountable for the difference of reaction between fishes in which the ears were intact, and those in which the eighth nerves had been cut.

VI. Discussion of Results.

The results of my experiments differ so essentially from those obtained by Kreidl ('95) that a further discussion of these differences is necessary. So far as reactions to sounds were concerned, Kreidl was unable to distinguish between normal goldfishes and individuals from which the semicircular canals with the attached parts of the ears had been removed. In my experiments, however, while normal fishes responded to sound in about 78% of the trials, those in which the eighth nerves had been cut, scarcely responded at all. The difference between these two sets of results was so great that I determined to repeat, with as much precision of detail as possible, Kreidl's experiments.

I tested several goldfishes, and, having found that they

responded well to the tuning fork, I operated on them in the following way. After etherizing the animals, I cut off the top of the skull, exposing the brain, and the vertical semicircular canals. I then seized the canals with forceps and drew them out bodily with the attached sacs and their otoliths, as Kreidl had done. I operated thus on four fishes, three of which recovered. After recovery, I tested them again with the tuning fork, and found that one responded to the sound about as well as before the operation, and that the two others responded somewhat less regularly than before, though in a still perfectly definite and unmistakable manner. Thus, since these fishes responded like normal individuals, my results confirmed in all essential respects those of Kreidl, and I came to the conclusion that there must be some fundamental difference between Kreidl's methods for the elimination of the ear, and mine. The method I generally used, cutting the eighth nerves, seemed to me a perfectly secure means of excluding the action of the ear. On the other hand, the withdrawal of the semicircular canals with the attached parts of the ear, as practiced by Kreidl, might well leave behind and intact parts of that organ, and thus be inefficient as a method for completely excluding the ear. To settle this matter, I made careful dissections of the ears of goldfishes. The ear of the goldfish is in all essential respects similar to that of Cyprinus, as described and figured by Retzius ('81, p. 78). The semicircular canals are of large size; the two vertical canals lie free in the brain cavity, while the horizontal canal is partially imbedded in the skull. The sac into which these canals open, the utriculus, is of medium size, and contains a large lenticular otolith. The utriculus, with its otolith lies free in the brain cavity and is the structure which is removed in connection with the semicircular canals in fishes which are operated on by Kreidl's method. But ventral to these parts, and largely imbedded in bone is another portion of the internal ear, which probably represents the combined sacculus and lagena. This is not removed, nor even seriously disturbed by the Kreidl operation. This deeper sac extends posteriorly and ventrally until that of the right ear nearly meets that of the left in the base of the cranium. Each sac contains two otoliths, one long and

rod like, lying for the most part in the saccular portion, the other lenticular in outline, and lodged in the lagena proper. The wall of this sac is supplied with branches from the eighth nerve and is so surrounded by bone that all attempts to remove it by pulling out the semicircular canals were complete failures. In the four fishes on which I operated by Kreidl's method, subsequent dissection showed these structures intact. Thus, his operation leaves uninjured a large part of the internal ear, in fact, just that part which, from comparison with the ears of higher vertebrates, would be expected to be concerned with hearing. I believe, therefore, that Kreidl's method of operating is defective, and the reason that the fishes upon which he had operated responded to sounds much as normal ones did, was not because in both cases the skin was stimulated, as he believed, but because his so-called "earless" fishes still retained intact a part of the ear which, as I have already shown, acts as an organ of hearing. That it is such an organ follows from the fact that when its nerve connections are cut, the responses to sound cease.

VII. Summary.

1. Normal goldfishes usually respond in a definite manner to sound-vibrations in water.
2. Goldfishes in which most of the skin has been rendered insensitive by cutting the nerves, and specimens from which the ears, except the saccular portion, have been removed still respond in an essentially normal way to sound vibrations in water.
3. Goldfishes in which the eighth nerves have been cut on both sides, thus eliminating the sacculi and lagenæ as well as the rest of the ear, seldom or never respond to sound vibrations in water.
4. Goldfishes possess the sense of hearing, and the portion of the ear concerned with this sense is the sac which probably represents the sacculus and the lagena of higher vertebrates.

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CERTAIN UNDETERMINED FACTORS IN HEREDITY AND ENVIRONMENT.

GEORGE J. PEIRCE.

In a paper read before the Botanical Section at the Pittsburg meeting of the American Association for the Advancement of Science [1] I suggested that certain factors of the environment were constantly ignored in such discussions of heredity as I had seen or heard. This paper constitutes substantially the last section of my book.[2] Since certain letters which I have recently received, make me feel that in this section I have expressed myself so concisely that my full meaning is not altogether clear, I take this opportunity to give somewhat ampler treatment to the subject.

The word *environment* is used ignorantly by everyone, for no one has ever succeeded in making a complete analysis of what is meant by this collective term. Furthermore, although we speak of an organism as reacting to its environment, it does not react to its environment as a whole but to each of one of the separate influences which are the factors of its environment. It is, therefore, very important to know what these factors are, and what are their effects. We know that if two of these influences are opposite and equal, there will be no visible reaction, although the organism will be affected by both. There may be internal results of these influences, results which, however, may not be perceptible. If one of these opposite influences be lessened or eliminated, the effect of the other becomes perceptible. We judge, then, the influence of the various factors which we are now able to distinguish from one another as constituting the environment, only by their perceptible effects. It is conceivable that some effects are so long deferred that they are coincident or at least contemporaneous with the effects of other and more recent stimuli. For this reason these long deferred effects may

[1] Abstract in *Science*, XVI. p. 137, 1902.

[2] Peirce, G. J. *Text book of Plant Physiology*, 279–83, New York, 1903.

easily be overlooked, or they may be perceived only incompletely and with difficulty, or they may be attributed to wrong causes. It is also conceivable that certain influences produce effects not because they are powerful, taking into account only short times of operation, but because they are prolonged.

This leads us to essay an analysis of environment. The environment of an organism is all, everything, that constitutes the world and the universe outside of itself. One may say that this definition is too comprehensive, that only *immediate* environment is meant when the word environment is generally used. Who can say that organisms and things are affected *only* by their immediate environment? In fact we know that the contrary is true in certain particulars. We know, for instance, that we are daily affected by the sun — a remote body — quite as much as by any part of our immediate environment. But we do not know all the radiations and other influences from all the heavenly bodies in the universe, the effects of these upon our earth as a planet, and what is upon it; and yet these radiations still unknown and unguessed, together with other unknown and unguessed factors of environment, may operate as regularly and as powerfully as any of the known and recognized factors.

Among the recognized factors of the environment are some, the effects of which are very imperfectly known, if they may be said to be known at all. These will be seen in their relations to other factors if an analysis, however imperfect, of the environment be given. Thus

Environment — all that constitutes the universe.	1. *The earth* — soil, rocks, waters, atmosphere; the components, conditions, contours, etc., of these. 2. *All other planets* — whatever conditions prevail upon them; their relative positions to the earth and to each other. 3. *The forces* emanating from and operating upon these — heat, light, electricity, mechanical forces (gravity, wind, waves, rain, etc.). 4. *All living things* — their parts, products, and habits.

If we go through the list of factors suggested by this scheme,

we shall see that, in spite of their diversity and oppositeness, we may bring them into an orderly classification. We may arrange them under these four headings — 1, unchanging, 2, variable, 3, occasional, 4, periodic. Among unchanging factors the following may be mentioned,[1] *viz.* the atmosphere, water, the force of gravity, the earth as a whole. Though these are not all of the unchanging influences I shall discuss only these four.

The earth's atmosphere, consisting of nitrogen (80%) and oxygen (20%), with only a small fraction of 1% of carbon-dioxide and other gaseous matters, possesses unchanging physical properties and exerts a pressure which varies only very slightly, taking only short intervals of time for the comparison, and varies not at all, taking long intervals of time. For example, the barometric pressures in any given locality are the same in this century as in the last, and though we may have "low" and "high" barometers at different times, these variations are very slight. The buoyancy, diversity, color, transparency, permeability, etc., of the earth's atmosphere are the same to-day as a "million" years ago, as far as we know, and though these qualities and the pressure of the atmosphere may change and may have changed during the lapse of the millions of years during which the earth is likely to exist and has existed as a planet, they are unchanging so far as millions of generations of living organisms, and so far as millions of series of lifeless things, are concerned.

The composition of the earth's atmosphere has changed but little, if at all. The proportion of carbon-dioxide may have been greater in an earlier time, but for uncountable ages the proportions have been what they are now. Let us suppose, however, that the proportions of nitrogen, oxygen, and carbon-dioxide have changed somewhat, taking the whole atmosphere into account, not a small part of it merely. If only the proportions were different, there would still have been nitrogen, oxygen, and carbon-dioxide in the air, and these gases themselves are unchanging. We cannot imagine some oxygen being any different from all oxygen; if we have carbon dioxide we have necessarily carbon-dioxide of the same composition and properties since the world began. The same of the inert gas nitrogen.

[1] See p. 280 of my "Text Book."

When experiments are instituted for the purpose of eliminating these substances, they fail, for it is out of the question to remove all nitrogen, oxygen, and carbon-dioxide even if all N, O, and Co_2 can be excluded at the beginning of an experiment, for N and O will be contained in the organism and Co_2 will be formed by it. Nevertheless, the living organism which is dependent upon oxygen for respiration, upon nitrogen to dilute the otherwise too destructive oxygen, and upon carbon-dioxide from which to manufacture food, will succumb in any experiment of more than brief duration in which the proportions of these gases are greatly different from those in normal air. In other words the physical properties of the atmosphere, its components, their composition and proportions, being and having for ages been what they are, living organisms represent reactions to these qualities and will not bear sudden change, whatever might be or may have been the result of gradual change, if there has been any.

Water is composed of hydrogen and oxygen in the proportions of two to one. It always has had the same chemical composition, structure, and properties, the same physical qualities. It is an indispensable constituent of living organisms and of many lifeless things. It is a weak acid and the most universal solvent known. Molecules and atoms of dissolved substances move about in it with considerable freedom, and where two volumes of water are separated from one another only by permeable or semi-permeable membranes, there is molecular or atomic movement both of water and of dissolved substance from the one volume to the other through the membrane. Water is then a medium in which ampler molecular and atomic movements are possible at ordinary temperatures, etc., than in many other substances. But the movement of the molecules and atoms of the solutes are independent of, though taking place among, the water molecules. The water remains the same, physically and chemically, whatever substances may be dissolved in it. The temperature of a solution of small volume may be different while solution is taking place, but ultimately the temperature of the solution, or of water holding nothing in solution, will be approximately that of its surroundings, other things being equal. The specific gravity of the solution will differ from that

of pure water, but the specific gravity of the water itself and of the solute itself are the same as they have always been, the specific gravity of the solution depending only upon these two.

With its physical and chemical properties unchanged, as an essential constituent of all living organisms and the medium in which necessarily the food materials and foods enter and move about and are chemically changed in the cell, water has exerted upon living things an influence as powerful and as persistent as have been its relations to the physical and chemical conditions and processes of lifeless substances since the beginning. Water can be eliminated neither outright nor by substitution from experiments with living organisms nor, for that matter, can it be eliminated from the majority of experiments with lifeless substances. It is a substance of universal occurrence, of uniform properties, of uniform action. It is truly one of the unchanging factors of the environment, to which living organisms necessarily react, for their composition, structure, nutrition, and activities depend upon it.

We come now to consider the effect of gravitation. The force of gravity acts upon every particle of ponderable matter on the earth as a direct pull toward the center of the earth. This pull is equal, at the surface of the earth, to 32.2 foot seconds^2, *i. e.* a body at the surface of the earth would fall in a vacuum at a rate increasing 32.2 feet a second per second. The force of gravity, operating upon every particle of ponderable matter, constantly exerts upon it this uniform force. The force increases or decreases inversely as the squares of the distances. But, as Newton showed, the force of gravity is not merely the attraction between the earth as a whole and other ponderable matters, but every portion of matter attracts every other portion with a force proportional to the product of their masses divided by the square of their distances apart.[1] The sum of the attractions toward the center of the earth equals the amount previously mentioned, 32.2 foot seconds^2, and this sum we may for the moment speak of as gravity without necessarily taking its components into account.

[1] Watson, W. *A Textbook of Physics*, p. 121. New York, 1900.

The attraction of gravity upon all ponderable matters is, however, opposed by the media in which they are. This is implied by the statement of the value of gravity at the earth's surface, for this statement specifies *in vacuo*. Every ponderable body is bouyed up (or supported) by a force equal to the weight of the fluid it displaces. This law of Archimedes concerns us as it applies to the air and to both fresh and salt water. Besides this we have the solidity and comparative impenetrability of the earth itself to reckon with, for the soil is capable of mechanically supporting much more than the weight of the parts of plants and animals resting upon or within it. Gravity is then opposed, partly or wholly, according to the medium in which the attracted object is.

The opposition to gravity varies from .0013 gr. per cc. in air at 0° C., and at ordinary atmospheric pressure, through 1.00 gr. per cc. in pure water and 1.20 gr. in sea water, to much more than the weight per cc. of any of the substances with which we ordinarily have to deal. Thus if we have a plant or animal or any other portion of matter weighing x grams in air, this matter would have a weight in pure water equal to x minus 1 gram for every cc. of volume. In sea water this would be $x - 1.2\ y$, in which y represents the number of cc. in the portion of matter. To take a concrete instance, suppose we have a block of wood, occupying a space of 9 cc. and weighing 10 gr. in air. This would weigh in water $10 - 1 \times 9 = 1$ gr.; in sea water this would be $10 - 1.2 \times 9 = 0.8$ gr. or, in other words, the block would float. In the same way the block would be completely supported, gravity would be completely offset, if the block were on or in the soil. But as the soil, the water, and the air do not come into direct contact with and are therefore not displaced by each individual part and particle of a portion of matter, there must be enough mechanical strength within the portion of matter to resist the force of gravity or the body would fall to pieces. We see then that though a body as a whole may be bouyed up by a considerable force which resists gravity, the component particles of the body are not necessarily so bouyed up but are subjected to the full attraction of gravity. Although the bouyancy of the medium

in which a plant lives makes a very great difference in the mechanical strength of the plant as a whole,[1] there is no discoverable difference in the structure and other properties of the protoplasm. This fact is what the foregoing discussion has lead us to expect; for upon the component particles of protoplasm the force of gravity operates unopposed by the bouyancy of air or water, except such water as is in the cell-sap; and as the force of gravity is continuous and uniform in operation, the living protoplasm is subjected to a continuous and uniform influence. Does it not react accordingly?

Again, the force of gravity, regarded both as the attraction of the earth as a whole as well as the attraction of each particle of matter for every other, has never been eliminated from any experiment. If it had been, can we imagine what would have happened? The force of gravity acts only in one direction. The slow revolution of a plant upon a horizontal axis by means of a clinostat, so that all its parts will be successively turned in this direction, and the opposition of centrifugal or other force to the force of gravity, yield interesting results in experiments in which these methods are employed, but they throw little or no light on the influence of gravity upon the component parts of the living structure. Until gravity is eliminated, not merely opposed, we cannot even guess what its influence is; but rather than ignore it, we may guess that its influence as a formative agent is as great as we now know its directive influence to be. And as we know that its directive influence is always the same, that plants of a kind under like conditions respond in approximately like ways, like times, and with like force to the action of gravity, sending their roots downward into the soil and their stems upward into the air, we must infer that in the formation of new protoplasm the component parts of this structure are affected always in the same way and that they respond to the constant and uniform force in constant and uniform ways.

It remains to add a word as to the earth as a whole as one of the continuous and uniform factors of the environment of living

[1] Peirce, G. J. A comparison of land and water plants. *Pop. Sci. Monthly*, LXIII, p. 239, 1903.

organisms. The earth is a spheroid whirling in space at a rate decreasing with inconceivable slowness. Its position with relation to other bodies of the solar and other planetary systems changes also with inconceivable slowness. It possesses a degree and a distribution of heat throughout its mass which changes also with wonderful slowness. The earth possesses size, structure, composition, compactness, and other physical and chemical properties which change so slowly that in the lapse of ages differences can scarcely be detected, and millions of generations come and go under exactly like influences.

Passing now from these unchanging factors to the living organism itself, we must see that every particle of protoplasm is affected by the components and by the properties of the atmosphere, by the physical and chemical qualities of water, by the force of gravity, and by the earth as a whole. Every particle of protoplasm since it came into existence as such, every molecule of every compound in it, and every atom in the molecule, has existed from its beginning on this earth under these conditions and subject to these influences. None of these influences has ever been eliminated by experiment, nor has experiment ever resulted in accomplishing any fundamental change in a living organism or series of living organisms. Man as an experimenter cannot control these influences but is controlled by them. Is he not controlled by them in every other relation in life? Is man any more controlled by these unchanging influences than any other living or lifeless thing?

In the living substance of sperm and egg the component parts, particles, molecules, and atoms, have been subjected to these unchanging forces, not only since coming together as the living structure, but before; and after sperm and egg fuse the same is true; and in the growth of the fertilized egg every particle of new material is formed, placed, and kept in place under these influences. From the beginning to the end of its career every individual plant and animal is subjected to these continuous and uniform influences. But so also is every other thing. And as we find all common salt crystals behaving alike and being fundamentally alike at the same time that they are unlike the crystals of all other substances subjected to these

same influences, so we find the plants or animals of a kind behaving and being in the main alike at the same time that they are unlike the plants and animals of all other kinds, although they are subjected to the same influences. In the diversity of composition and adjustment to these forces we have a physical reason for the diversity of behavior of different animals, plants, and lifeless things. They are all influenced by these forces; what they are represents their reactions to these and to other forces. The fundamental likeness of parent and offspring represents the continuity of substance and of influence; the superficial differences represent the different influences to which they have been subjected and to which they have reacted. Not all common salt crystals are of exactly the same size. Not all the puppies of a litter are exactly alike. But the salt crystals are fundamentally alike, and so are the puppies. With their vastly greater complexity — considered merely chemically for the moment — one should expect puppies to vary more than salt crystals. But neither salt crystals nor puppies vary so far as not to be salt crystals or puppies; the continuous influences conserve their fundamental characters.

In this discussion two things have been assumed — the continuity of substance from parent to offspring, and the irritability the power of reaction, of this substance to the various factors of its environment. These two facts are essential to heredity. My contention is merely that in the continuous, unchanging factors of the environment we have forces, influences, stimuli, under the operation of which the living substance came into existence, under which it continues to exist, and to which it continuously and unchangingly reacts. These influences are factors in the environment, but at the same time, like irritability, they are factors in heredity. The clearer our conception and the fuller our knowledge of the irritability and the power of reaction of living organisms to external stimuli, the smaller the mass of unexplained though not unexplainable phenomena for which we shall make heredity accountable.

Stanford University,
February, 1904.

ON THE DENTITION OF RHYNCHODUS AND OTHER FOSSIL FISHES.

C R. EASTMAN.

AMONGST Palæozoic chimæroids the complete dentition is known in at least two species of Ptyctodus, two of Rhynchodus and one of Palæomylus. These genera are all included in the family Ptyctodontidæ of the Devonian, and present for comparison with recent chimæroids a single dental plate on each side in the upper jaw, with a corresponding pair biting against the outer side of these (as shown by marks of contact) in the lower jaw. The question therefore arises whether the unique dental plate on each side in the upper jaw of ptyctodonts is homologous with the so-called "premaxillary" of Chimæra, Callorhynchus, Rhinochimæra, etc., or with the so-called "palatine plate" of the latter, or with both premaxillary and palatine taken together.

This question appears to be answered conclusively in the case of Ptyctodus, from which the modern type of dentition is derived by pushing the low and elongate upper dental plate further back in the mouth, and introducing a "premaxillary" or "vomerine" tooth in front of it. In all cases the lower dental plate is vertically deeper than the upper, and rises into a prominent beak anteriorly. It is also characterized by having a descending process at the symphysis, which is more accentuated in the fossil than in recent forms. This process bears a triangular groove or excavation on its inner face, the roughened surface of which indicates that it was occupied by cartilage, since there was no sutural union at the symphysis. That this was the case is self-evident, for the anterior beaks could not have closed outside the upper dental plates when the mouth was shut unless the lower ones were mutually separated by a slight interval.

In a recent communication by Jækel,[1] it is stated that "von

[1] Jækel, O., Ueber Ramphodus etc., *Sitzungsber. Ges. naturf. Freunde*, Berlin, 1903, pp. 383-393.

der Zahnform und dem Gesammtgebiss von Ptyctodus wissen wir noch nichts genaueres," and it is thought that "vielleicht ist Ptyctodus schon ein echter Vertreter der sechszahnigen Holocephalen, ... die wohl von den *Coccosteiden* abstammen mögen." This author's evident unfamiliarity with the Ptyctodus type of dentition is no doubt responsible for his confusion of the upper and lower dental plates of a species of Rhynchodus from the Upper Devonian of Wildungen, Waldeck, and for the impossible suggestion that the nasal capsules projected into the triangular incisions which occur in the descending process of the mandibular dental plates.

That which is commonly interpreted as the *lower* dental plate of Rhynchodus, Jækel homologizes with the "premaxillary tooth" of Chimæra; and that attributed to the *upper* jaw of the former, Jækel supposes to have functioned as a mandibular element. Referring to the lower dental plate from the Eifel Devonian described by F. v. Huene under the name of *Rhynchodus emigratus*, Jækel states that he prefers to regard it as a "Præmaxillarzahn," and notes its close resemblance to the Wildungen teeth called by him *Ramphodus tetrodon.* So far as one may judge without having compared the original specimens, no essential differences exist between these forms and the earlier described *Rhynchodus major* and *R. rostratus*[1] respectively. An illustration of the Wildungen dental plates is given in the accompanying text-figure 1, slightly modified after Jækel, that is to say, the latter's figure is inverted, and the upper dental plate is thrust forward so as to protrude beyond the lower.

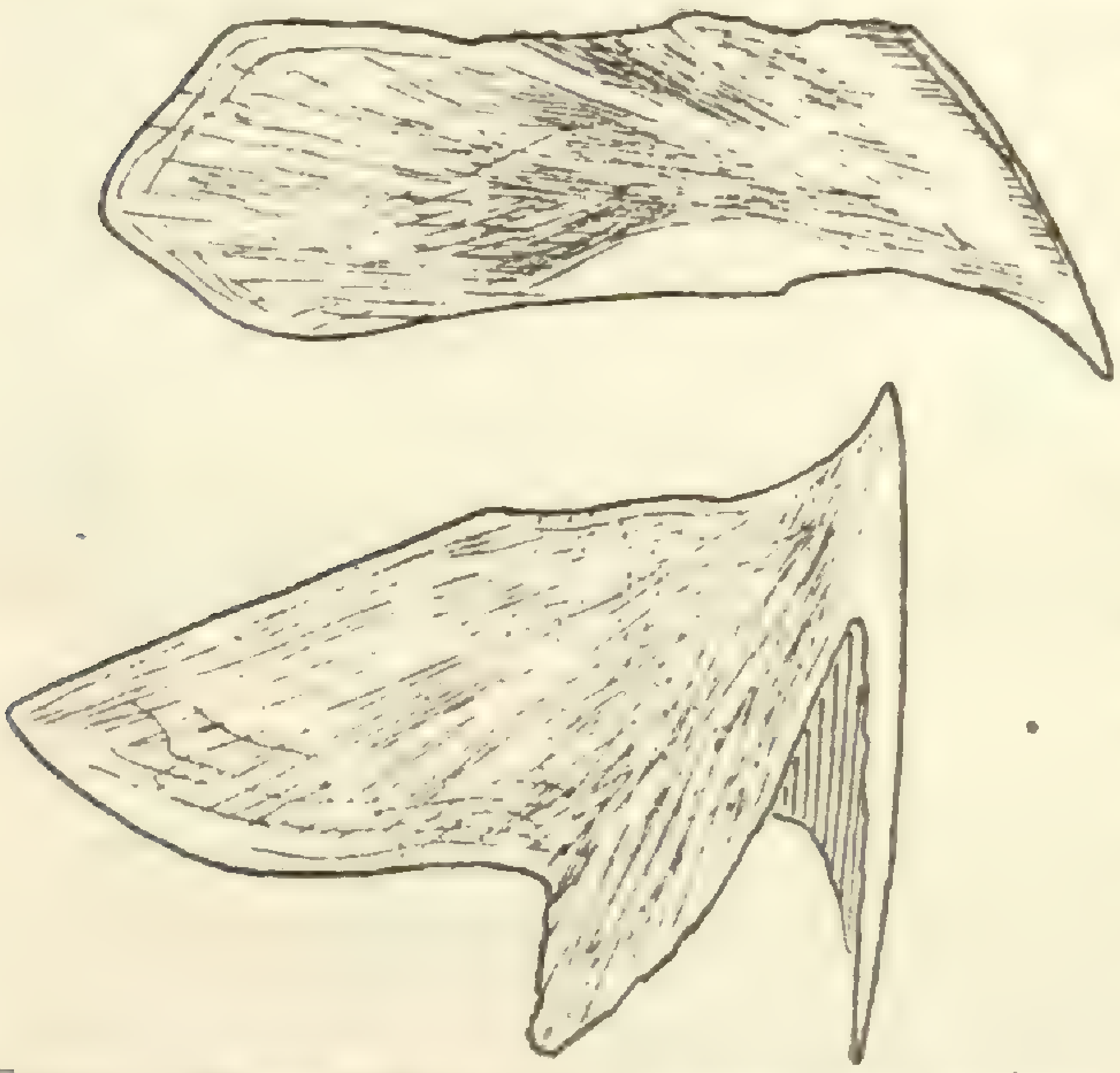

Fig. 1.— Left upper and lower dental plates (inner aspect) of *Rhynchodus major*, from the Upper Devonian of Wildungen (after Jaekel). × [illegible].

[1] Eastman, C. R., Dentition of Devonian Ptyctodontidæ. *Amer. Nat.* vol. XXXII, p. 487, 1898.— *Centralblatt für Mineral.*, 1900, p. 177.

Rhynchodus pertenuis, sp. nov.

Dental plate narrow and elongate, with sharp and extended cutting edge and knife-blade cross-section; anterior beak prominent, no symphysial process, external surface smooth.

The unique dental plate upon which this species is founded was obtained from the Chemung of Franklin, in Delaware County, New York, and is preserved in the State Museum at Albany, where the attention of the writer was called to it by Dr. J. M. Clarke, State Palæontologist, but not in time to include its description with other fish remains already made known from the same locality.[1] The general outline and proportions of this form differ from those of all other species, and the absence of a symphysial process is a very unusual feature. But for the trenchant cutting edge and narrow cross-section, the

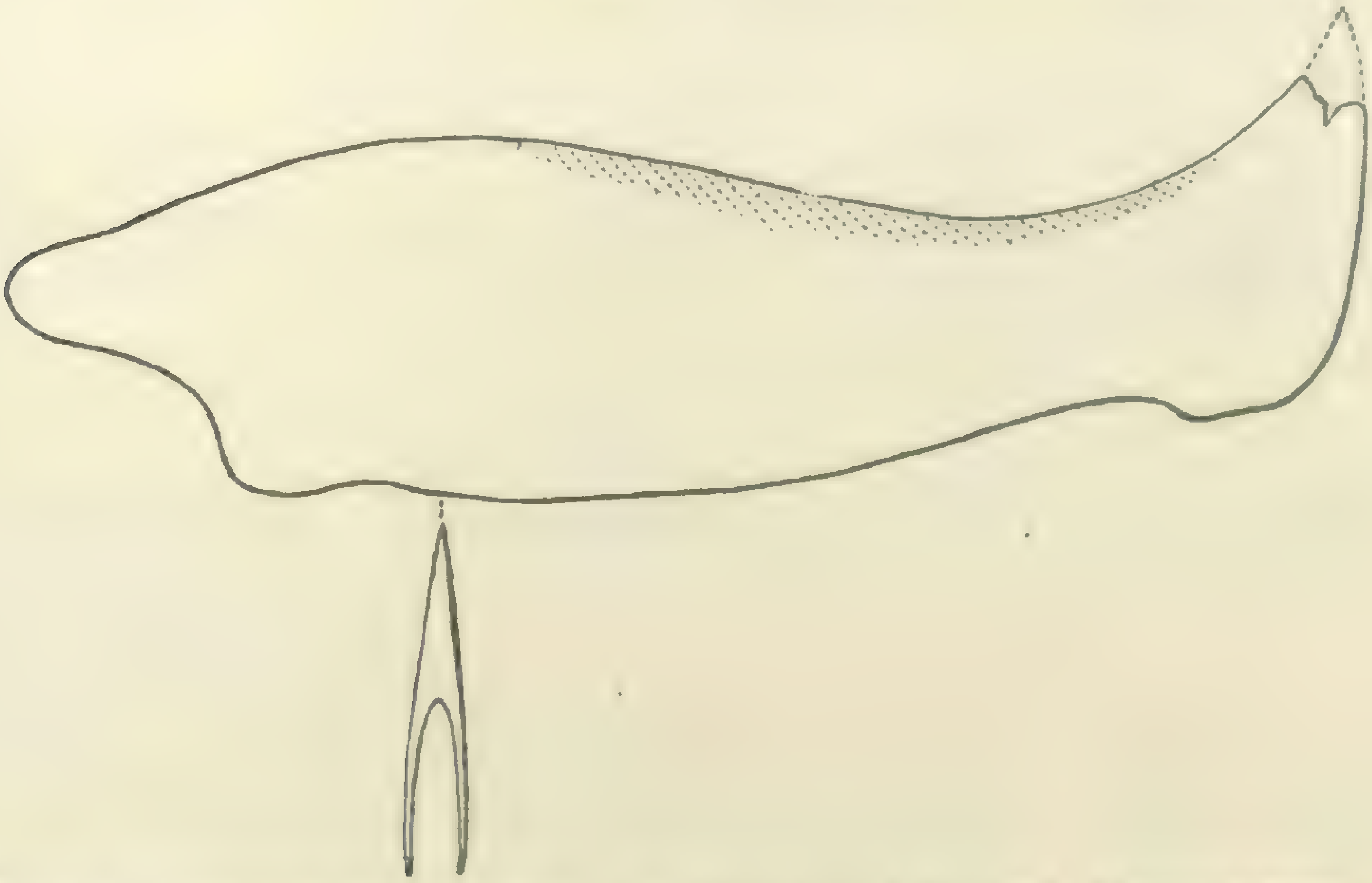

Fig. 2.—*Rhynchodus pertenuis*, sp. nov. Mandibular dental plate, · [illegible]. Chemung group: Delaware County, New York.

specimen might be readily mistaken for a lower dental plate of Ptyctodus, instead of Rhynchodus. That it is properly a mandibular element, and referable to the latter genus, seems to admit of no question. The hollow along the base indicates the extent to which the plate was buried in the supporting cartilage of the jaws. The total length is 9 cm.

[1] *Ann. Rept. State Geol. N. Y.* 1897 (1899), pp. 317–327.

Fragments of chimæroid jaws have been previously reported from the Chemung of New York State by Clarke, but no specific identifications were attempted by him. At best this class of remains appears to be very rare in the eastern province, Ptyctodus and Rhynchodus being the only genera that are known from the New York Devonian. An undescribed species of the former occurs in the Corniferous limestone of Le Roy, and *P. calceolus* is apparently represented in the Hamilton stage at Eighteen Mile Creek, near Buffalo. Detached tritors from both of these localities are preserved in the Museum of Comparative Zoölogy at Cambridge.

Onchosaurus Gervais.

Syn. Ischyrhiza Leidy; Gigantichthys Dames.

A comparison of the type specimens of Gervais' *Onchosaurus radicalis*[1] and Leidy's *Ischyrhiza antiqua*,[2] the former being preserved in the collection of the School of Mines at Paris, and the latter in the American Museum of Natural History in New York, leaves no room for doubt that they are generically, and probably also specifically identical, in which case Leidy's title must be abandoned. The original of Gervais' description, together with one or two duplicates, was derived from the Upper Cretaceous of Meudon, near Paris, and regarded through error as of mosasaur nature. The identical form occurs also in the Mæstricht Chalk, a remarkably fine specimen from this locality being preserved in the Paris Museum of Natural History.

The type of Leidy's genus, *I. mira*,[3] was founded on a unique tooth from the Cretaceous Greensand of Burlington County, New Jersey, and supposed by the author to represent a Teleost fish related to Sphyræna. The original has never been figured,

[1] *Zoologie et Paléontologie Françaises*, vol. I, p. 262, pl. lix. fig. 26, 1852.

[2] *Proc. Acad. Nat. Sci. Philad.* vol. VII, p. 256. 1856. — Emmons, E., *Report North Carolina Geol. Surv.*, p. 225, figs. 47, 48, 1858. — Leidy, J., in F. S. Holmes' *Post-Pliocene Fossils of South Carolina*, p. 120, pl. xxv, figs. 3–8. 1860.

[3] *Proc. Acad. Nat. Sci. Philad.* vol. VII, p. 221. 1856.

and its present whereabouts are unknown. The so-called *Ischyrhiza antiqua* is stated by Leidy to occur in New Jersey, North and South Carolina, New Mexico and Mississippi, but the differences between this and *I. mira* are inappreciable, and the two were finally pronounced identical by their author. Certain hypural fans similar to those accompanying Protosphyræna in the English Greensand have been theoretically associated with Ischyrhiza, but with questionable propriety.[1] No reasons have been assigned for making this association, and other considerations militate against it, hence it appears advisable to exclude these fans altogether from the same genus.

The wide geographical distribution enjoyed by Onchosaurus is shown by its occurrence not only in Europe and America, but also in the Upper Cretaceous of Egypt. In 1887 a tooth differing from the type species only in unimportant particulars was described by Dames[2] from the Senonian of Gizeh under the name of *Titanichthys pharao*, the generic title being subsequently changed to Gigantichthys. Dames' figure was copied by Zittel in his "Handbuch",[3] and the two authors agree in placing this form in the vicinity of Enchodus, although "Ischyrhiza" is referred by Zittel in the same work to the Esocidæ. The latter position was first suggested by Cope, and is likewise adopted by O. P. Hay.[4] It will be seen, therefore, that there is good authority for regarding Onchosaurus as one of the early forerunners of the pikes.

CAMBRIDGE, MASS.

[1] Cope, E. D., Vertebrata of the Cretaceous Formations of the West, p. 280. 1875.— Clark, W. B., *Bull. U. S. Geol. Surv.* no. 141, p. 60, pl. vii, fig. 2a. 1897.— *Maryland Geol. Surv., Eocene*, p. 112, pl. xii, fig. 8. 1901.

[2] *Sitzungsber. Ges. naturf. Freunde*, Berlin, p. 70, with figure, and p. 137. 1887.

[3] *Handbuch der Paläontologie*, vol. III, p. 269, fig. 274. 1890.

[4] *Bull. U. S. Geol. Surv.* no. 179, p. 398. 1902.

FURTHER INSTANCES OF PARIETAL DIVISION.

ALES HRDLICKA.

SINCE the publication of my monograph on "Division of the Parietal Bone in Man and other Mammals,"[1] there appeared in print three other direct or indirect communications on that same subject by Frasetto,[2] Schwalbe,[3] and Le Double.[4]

The new instances of the anomaly reported by these authors are as follows:

A. In human adults.— 1. An antero-posterior complete division of the left parietal in an "adult Savoyard" (Le Double);

2. A complete vertical division, "originating from the sagittal point" and "terminating in the inferior border" of the right parietal, in the skull of an adult male (Le Double). The race of the individual is not mentioned and the description leaves much in doubt.

3. A division in the right parietal of a "heavy, sclerotic," skull of a male Egyptian. The division runs from the coronal to the posterior third of the inferior border, and connects with a trace of a vertical division (Frasetto). As the author states that the usual sutures, even the parieto-temporal, are sinostosed, there is great uncertainty as to the character of the division; it suggests a traumatism more than an anomalous suture.

B. In human children and fœtuses.— 1. An antero-posterior complete division in the right parietal of a seven year old child, sex and race unknown. Skull hydrocephalic (Schwalbe).

2. An antero-posterior complete division in the left parietal

[1] *Bull. Amer. Mus. Nat. Hist.*, Vol. 19, Art. VIII, pp. 231–386, N. Y. July, 1903.

[2] Notes de Craniologie comparée. *Ann. sci. nat.*, pp. 148–187. September. 1903.

[3] Ueber getheilte Scheitelbeine. *Zeitschr. Morph. Anthrop.* 1903. pp. 1–74. Stuttgart.

[4] *Traité des variations des os du crane de l'homme.* Paris, 1903. "Parietal." pp. 101–141.

of a new born child. Sex and race unknown. Skull hydrocephalic (Schwalbe).

3. An antero-posterior complete division in the right parietal in a female new born child (Frassetto).

4. An anterio-posterior complete division in the right parietal of a six months' fœtus. Sex and race not given (Frassetto).

5. An antero-posterior complete division in the right parietal

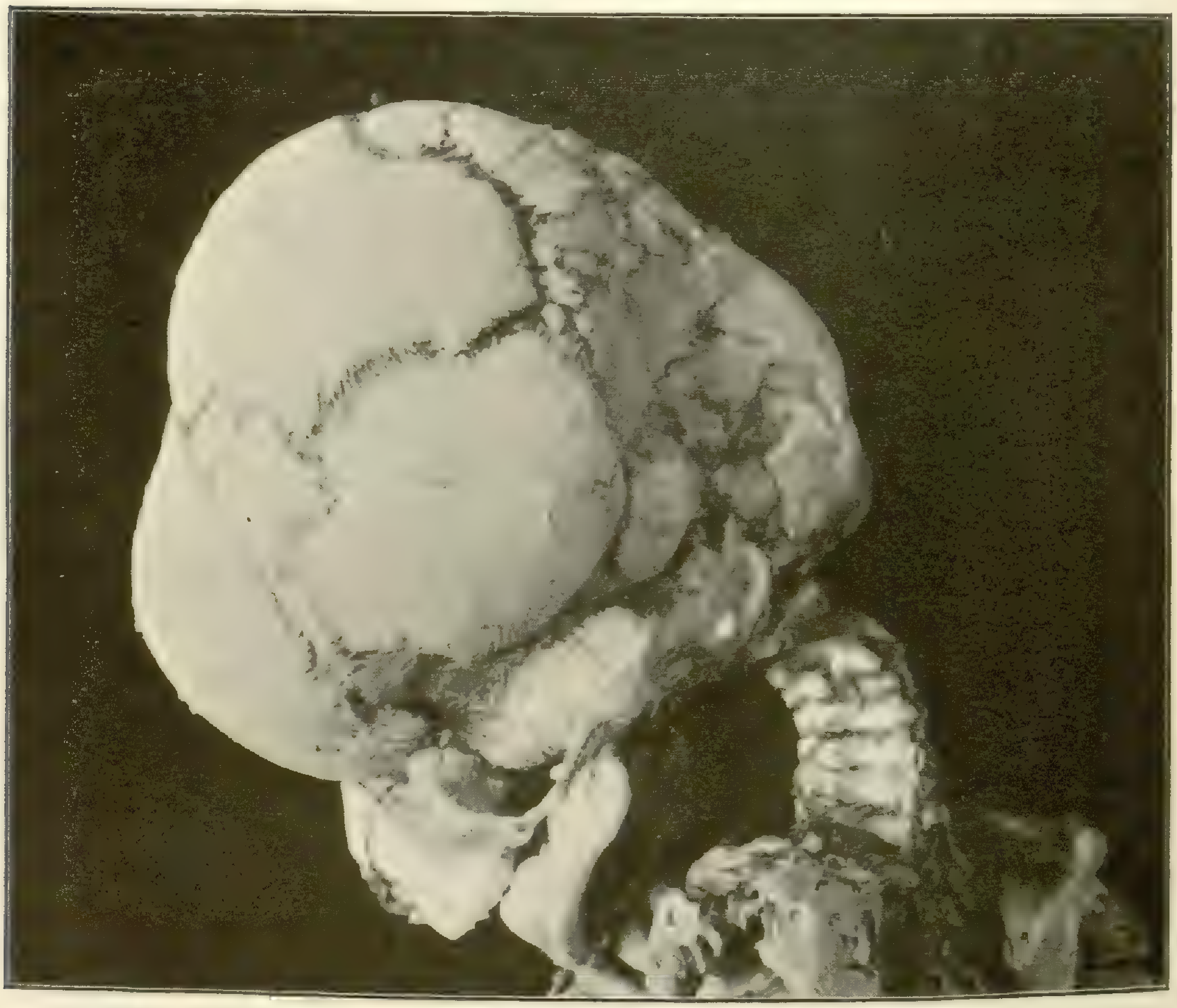

FIG. 1.— Anomalous division of the left parietal bone in a rachitic human fœtus.

of a four to six months' fœtus, sex and race not given (Frassetto).

6. A separation of the mastoid angle of the left parietal in an infant. Sex, age and race not given (Frassetto).

C. In Primates.— 1. *Simia sabea* (Cercopithecus). Right parietal divided into four parts. This same case, apparently, is reported by both Frassetto and Le Double.[1]

[1] Frassetto says the skull is No. A–1341 of the galeries of comparative anatomy of the Museum of Paris, while Le Double reports his specimen as No. A–134. in the Museum of Comparative Anatomy, Paris. Neither account is a thorough one.

2. A vertical, curving, complete suture in the left parietal of a young Semnopithecus (Frassetto).

3. A vertical, complete suture in the right parietal of a *Cercopithecus callitrichus* (Frassetto).

4. An oblique, vertical, complete, but synostosed suture in the right parietal of a *Macacus sinicus* (Frassetto).

5. A separation of the sphenoidal angle of the right parietal in a Mormon maimon (Frassetto).

D. Other Mammals.— 1. *Ursus americanus*, young. The

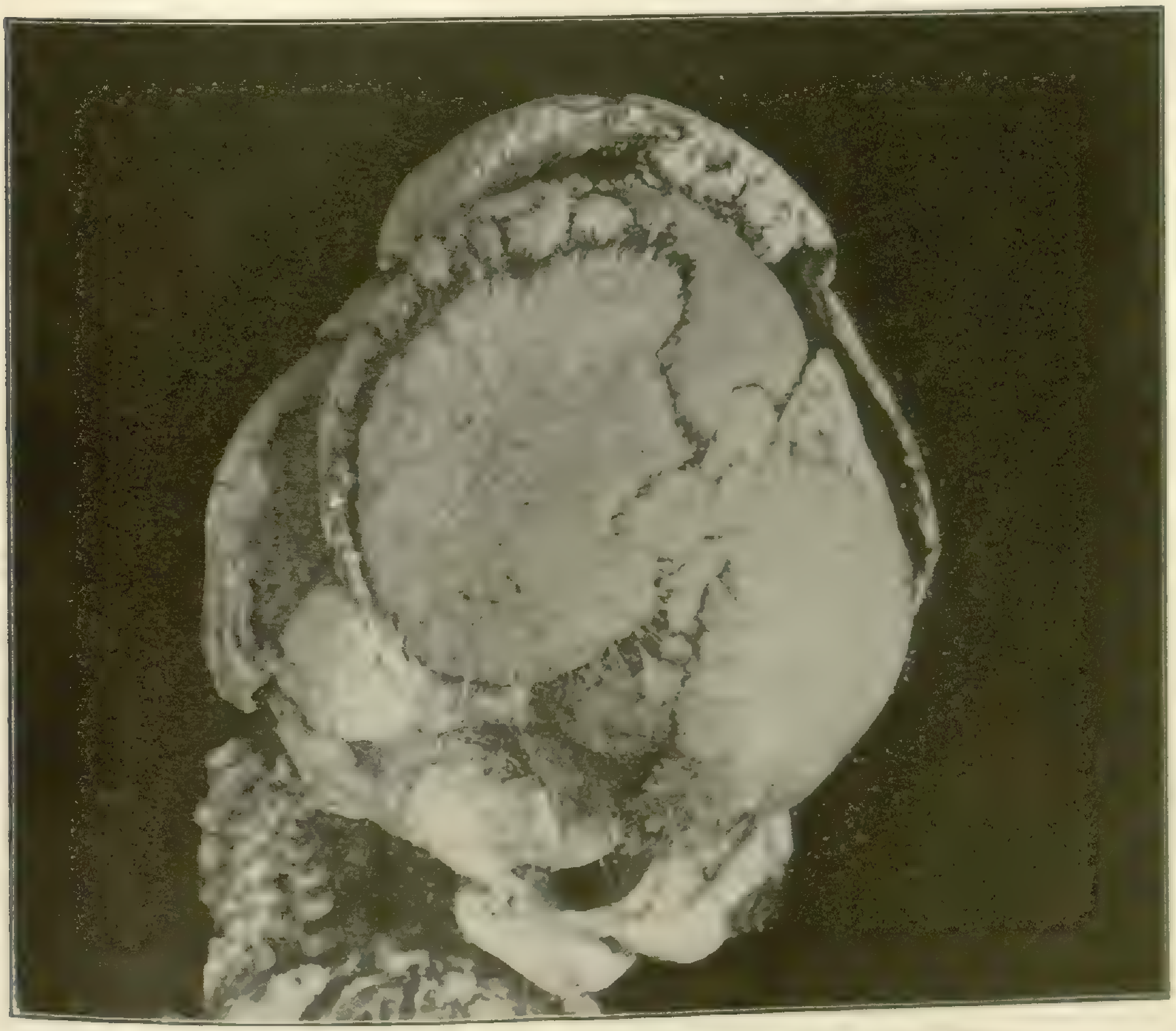

Fig. 2.— Abnormalities of the right parietal in the rachitic human fœtus

left parietal is divided into four irregular pieces. On the right is found a separation of the sphenoidal angle and an oblique, incomplete suture running downward and forward from the sagittal border near the lambda. This case, too, is reported independently and imperfectly by Frassetto and Le Double.

The new cases of complete parietal division that came to my attention since July, 1903, are briefly these : —

B. 1. A human fœtus,[1] of white parents, born at term, ninth pregnancy. The child weighed three pounds and lived four days. Whole skeleton highly rachitic.

Both of the parietals, besides other bones of the skull, show considerable modification. (Figs. 1 and 2.)

The left parietal is divided into two by a narrow and somewhat irregular membranous space running antero-posteriorly, very nearly parallel with the line of the sagittal junction, which is also membranous. The upper portion is slightly higher than the lower, its maximum height, measured by a tape, being 4.2 cm., while that of the lower piece is 3.8 cm.

The anterior third of the dividing space is very wide, forming a large fontanel, and this is filled with one large and one smaller secondary bones. Posterior to the two portions of the parietal and between these and the occipital, from the sagittal line to the mastoid, is another space, in the mean 2.5 cm. broad, somewhat narrower inferiorly than superiorly, filled with various sized secondary ossicles.

The squamo-parietal junction and much of the fronto-parietal are still membranous.

On the right there is plainly but one parietal. This is comparatively small and somewhat irregular. In about the middle of the anterior border is a V shaped defect (fontanel), corresponding to that on the left, and filled with a moderate sized secondary bone The whole fronto-parietal junction is occupied by a row of such bones and the same is true of the sagittal, parieto-occipital and to a less degree the squamo-parietal spaces. One of the secondary bones occupies the antero-superior angle of the parietal area and is of a large size, but is plainly of an accessory character, formed from an accidental accessory focus of ossification. Another larger bony piece occupies the asteric angle.

The skull has been somewhat deformed in preparation or drying and the posterior parietal region on each side is depressed, showing on this account but imperfectly in the illustrations. The bregma fontanel is large and partly filled with small sec-

[1] No. 9754, Army Med. Museum; gift of Dr. M. D. Spackman.

ondary ossicles. The occipital bone shows the ordinary at this age separation of the squama, exoccipital and basal portions. The development of the temporal bones, particularly the squamæ, is much retarded.

This case is of interest in several ways. It is another instance where the anomaly of parietal division is associated with a pronounced pathological condition of the skull. Such association, particularly with hydrocephalus (some degree of which may have existed even in the skull under consideration), is so common in the children and fœtal series of the cases reported that the causal relation of these pathological conditions with the divisions becomes more and more firmly established. They, of course, play the role of the exciting cause only, the fundamental condition which makes a parietal division possible being the presence of two starting foci or centers of ossification of the bone. In this connection one is forcibly reminded of the apparent rarity of pathological conditions in the adult human and also in the ape and monkey skulls with parietal divisions. Even if it be granted that much may right itself during the growth of the skull, it would seem that at least some of the parietal divisions in man and most of those in lower primates must be due to other exciting causes than rickets or hydrocephalus.

The second point of interest in the present case is the presence of two large and plainly *accessory* bones (antero-superiorly and postero-inferiorly on the right) which in an adult skull could easily be taken for primary portions of the parietal. As can be seen in the illustration the small true parietal on the right side shows a marked cleft near the middle of the anterior border. This cleft, it has been amply demonstrated before, is a remnant of the original membranous space between the upper and lower parietal centres. We had here, then, the two normal elementary foci of the bone and in the usual position. But the growth of the already fused primary parietal, due to rachitis, was retarded. Such a retardation in any of the bones of the cranial vault and from any reason leads invariably, undoubtedly through some trophic impulse which regulates the cranial growth, to the appearance of more or less numerous secondary foci of ossification, from which result various sized supple-

mentary, compensatory bones, commonly known as the wormians. Some of these secondary centres, as a rule those in localities where the greatest deficiencies exist, which is at the fontanels, show often more vital strength than others, enlarge to more striking dimensions and eventually, meeting and articulating with the advancing primary parietal, seem to represent and are mistaken for separated parts of this bone. There is no doubt but that the great majority of the "bregma," "human interparietal," and supraoccipital bones, as well as many of the "separated angles of the parietal" belong to this category. The difference between the compensatory bone and one that arose from lack of fusion of the primary centres is morphologically and particularly etiologically important.

The third point that the case at hand illustrates very handsomely is the possibility of a formation of a vertical parietal suture without any division, or totally independent of a division, of the primary parietal. Had the conditions in this skull advanced to a full development and particularly into adult life, before which period many of the closely packed wormians fuse, we should have had, unless an early synostosis obliterated the

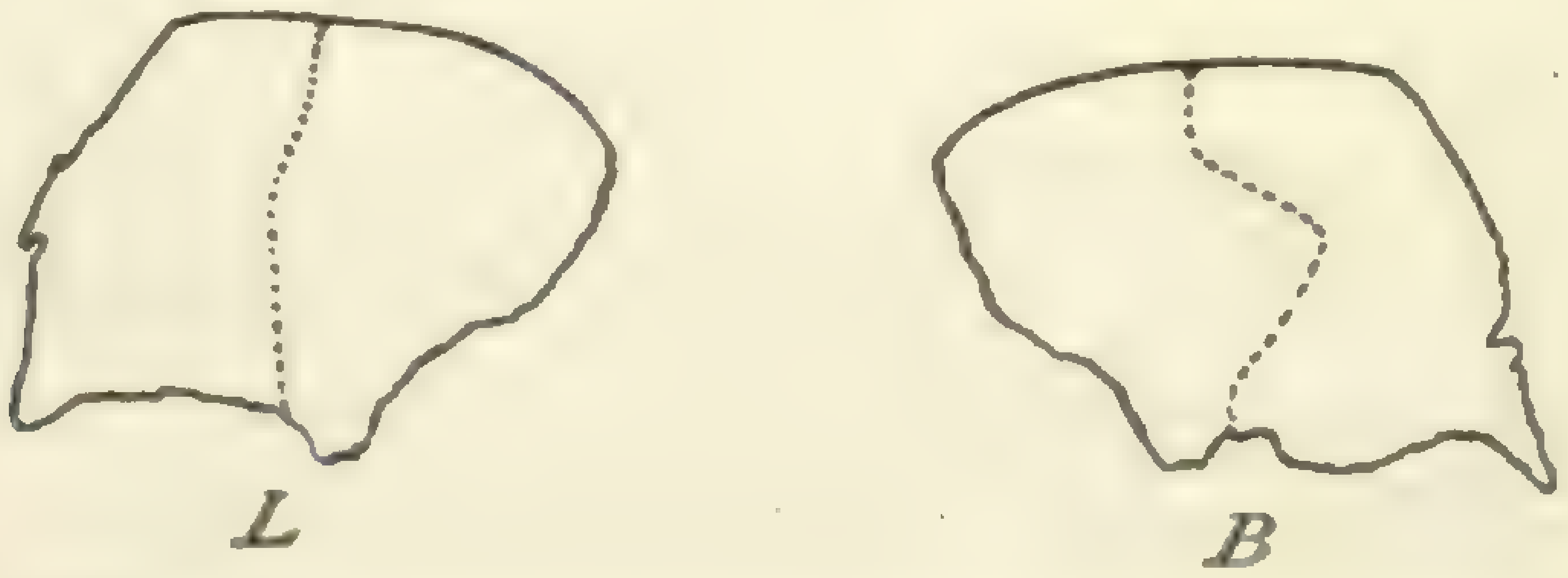

FIG. 3.—Bilateral, nearly obliterated vertical parietal division in a Hapale.

feature, a case very much like that of Fusari, which posess, I am inclined to think, falsely as an example of vertical parietal division in a human individual.

C. 1. Hapale, male, adolescent (No. 36,222, Dept. of Biology, U. S. Nat. Mus.). Skull apparently normal, symmetrical. The ordinary sutures all open. Each parietal shows a plain trace of a complete, vertical, now synostosed division. On the left the division began superiorly 9 mm. posterior to the bregma and 13 mm. anterior to the lambda, ran, slightly curving and nearly parallel to the coronal suture, to the temporal ridge, then

made a slight bend backward and ended a short distance anterior to the squamo-mastoid junction. The right division began one mm. posterior to that on the left and running a much more angular course terminated in the same relative position as that in the opposite parietal (Fig. 3).

2. *Cebus apella*, male, adolescent (No. 59,298, Dept. of Biol., U. S. N. M.). Skull slightly asymmetrical, surface of bones irregular (rachitis?). No injury. On the left side a serrated, vertical-oblique suture separates a large portion of the antero-inferior angle of the parietal. The anomalous suture begins anteriorly 10 mm. from the point where the coronal meets the fronto-malar suture (there is a bilateral malo-parietal articulation), and 36 mm. from the bregma; it ends inferiorly 14 mm. posterior to the meeting of the malo-parietal with the spheno-parietal suture and 51 mm. anterior to the asterion. On the right side 14 mm. above the point of meeting of the coronal and the frontal suture is a small v cleft in the parietal and from this runs backward and slightly downward a 4.5 mm. long fissure. On the same side exists a 13 mm. long, slightly wavy, vertical fissure in the frontal squama. It rises vertically from the fronto-

FIG. 4.—The left parietal of a *Cebus apella*, showing a separation of the antero-inferior angle.

malar suture and reaches the frontal part of the crest of the temporal muscle. There is no trace of any violence that might account for this fissure. (Fig. 4.)

The total number of ape, monkey, and lemur skulls examined in the U. S. National Museum was 316. A large majority of these skulls are those of adults, but no specimen was considered in which all the normal sutures of the cranial vault were not

plainly traceable. The varieties, and the parietal divisions found, are as follows:

11	Lemurs	no division.
6	Galagos	" "
1	Tardigradus	" "
11	Propitheci	" "
1	Gorilla	" "
1	Orang	" "
1	Chimpanzee	" "
11	Gibbons	" "
23	Semnopitheci	" "
27	Presbytes	" "
8	*Simias concolor*	" "
1	*Nasalis larvatus*	" "
1	*Cynopithecus niger*	" "

82 Macaques no division in 79; in one, from Siam (No. 83,-274), there is in the right parietal above the sphenoidal angle a moderate size, curving, antero-posterior fissure; in one *M. rhesus* (No. 83,476), a vertical fissure runs on the left from the posterior third, on the right from the posterior fourth of the sagittal border towards near the middle of each parietal; in another, *M. rhesus* (No. 63,379), there is on the left parietal a trace of what was probably a complete vertical suture, running from the middle of the sagittal to the inferior border of the bone.

15 Cynocephali no division in 14; in one (No. 22,904), young, there is a partial vertical division in each parietal, left 10 mm. long and starting from between the anterior and middle thirds, right 19 mm. long and starting from between the third and last fourths of the sagittal border.

1	Colobus	no division.
5	Cercocebi	" "

19 Cercopitheci no division in 18; in one (No. 36,277), there is in the right parietal a vertical-oblique fissure which begins superiorly between the anterior and middle thirds of the sagittal border and runs to the parietal eminence.

34 Cebi no division in 32; in one (No. 59,298, described in

detail), a suture separates the left sphenoidal angle; in one (No. 82,779), there are two fissures, each 10 mm. long, in the superior third of the coronal border of the left parietal.

9 Hapale no division in 8; in one (No. 36,222, described in detail) a bilateral complete vertical division.

4 Midas . . . . no division.

1 Aotus . . . . " "

1 Brazil monkey No. 984, there is a 4 mm. long, vertical fissure in the superior border of the left parietal, slightly anterior to its middle.

7 Chrysothrix . . . . . no division.

2 Lagothrix . . . . . " "

10 Mycetes . . . . " "

4 Alonata . . . . " "

1 Nictipithecus rufipes . . . . " "

16 Ateles no division in 14; in one *A. geoffroyi* (No. 8,974), young, the left parietal shows two incisures, one horizontal, 10. mm. long, just above the lower third of the coronal border, and one vertical, 15 mm. long, running from the middle of the sagittal border. In one *A. ater* (No. 63,425), there is in each parietal, a short distance anterior to the middle of the superior border, a vertical, 9 mm. long fissure.

The main facts accentuated by the examination of this National Museum series of monkey skulls is the relative rarity of parietal divisions in adult specimens. The condition in all forms should be sought for preferably in the young. As a rule, synostosis is later at least in some, and at times in all, of the normal parietal articulations than in the abnormal divisions.

U. S. National Museum.

COMPARISON OF THE PROVISIONAL SCHEMES OF THE CLASSIFICATION OF BIRDS.[1]

R. W. SHUFELDT.

It is not my intention in the present paper to offer any scheme of my own for the classification of birds, although it is a question that has long engaged my attention, and I hope soon to publish, in another connection, a provisional scheme, presenting what I take to be a natural taxonomy of Aves in so far as it is now understood. My only object here is to offer a few brief remarks upon the more prominent schemes for the classification of birds which have been put forward within recent times, and in a way compare the views of their sponsors. Careful recapitulation, undertaken from time to time, is always an advantage to any science, especially if that recapitulation is made along comparative lines and according to scientific methods. In other activities in which men engage, the benefits attaching to the occasional calling of a halt, with the view of taking account of the progress made; to making sure that advancement is being made along the right lines, has always been recognized. This, too, holds true in the domain of ornithological science. In fact, those who make the greatest, the surest and most substantial progress in anything are the ones who command a digested and available knowledge of all that has been previously accomplished in the field in which they labor.

It will be a red-letter day for our science when any species or subspecies of birds is and are known throughout the world by the same name, vernacular or scientific. That is, the opinion in regard to nomenclature will be unanimous. There will be equal rejoicing when that day arrives, when a unanimity of opinion exists in regard to the classification of birds. It is quite possible that many species now existing in the world's avi-

[1] Read by title at the twenty-first Congress of the American Ornithologists' Union, held at the Academy of Natural Sciences of Philadelphia, 1903.

fauna will, when that time comes, be extinct. With nomenclature I have nothing to do. Names are the inventions of men, whereas on the other hand, the relationships existing among birds in nature are actual, and in so far as invention enters here, it can only be in the form of printed, diagrammatic, or other device, to convey to the eye and mind what our conceptions of those relationships are. We may change names at any time and invent new ones *ad libitum*, but not so real relationships. These are fixed, and it remains for us to ascertain what they really are, and express them in the simplest terms. This is a matter of time, and I know of but two ways by means of which a consensus of opinion of ornithologists can be arrived at. First, by our mastering the morphology, geographical distribution, habits and life histories of all existing forms, and the osteology and other remains of all extinct ones within our ken; second, by the meeting of competent ornithologists in congress to discuss anything that touches upon the classification of the Class, and especially of the visible means of representing digested ideas in regard to it. Much could be accomplished by an international congress like the Second International Ornithological Congress which met at Budapest in 1891.

Of all the papers read at that Congress, none attracted more attention nor has been more useful or more closely studied since, than the paper read by Dr. R. Bowdler Sharpe, entitled "A Review of Recent Attempts to Classify Birds." It is the best thing of the kind extant and is so well known to ornithologists the world over as not to need further comment. I acknowledge with pleasure the assistance it has been to me in preparing the present paper. Apart from the many sound suggestions made by Dr. Sharpe in that address, and the historical lore it places at one's command, the main assistance I have derived from it has been the opportunity it affords me to study and to compare so many of the schemes of classification that have been proposed from time to time. To be sure, there now exist a number of other avian classifications. I refer especially to the classification of Aves proposed by Cope in 1889, entitled "Synopsis of the Families of Vertebrata," *The American Naturalist*, Vol. XXIII, pp. 849–877, and also to the taxonomic scheme brought forward by Gadow in

his contribution to the *Proceedings of the Zoölogical Society of London* for the year 1892, entitled "On the Classification of Birds," (pp. 229–256). So far as I am at present aware, Cope's and Gadow's classifications of Aves are the only two of any importance that have been published since Sharpe gave us his brochure cited above. If this be true, there has been no completed classification of this Class of Vertebrates published for over ten years. There have, however, been a number of such schemes partly completed and partly published, as for example the classification of birds as set forth in Sharpe's *Hand-List of Birds*, now passing through the press, and of which but one part remains to be issued. This admirable and most useful work will contain one of the most elaborate classifications of birds ever published. It is especially valuable inasmuch as Sharpe belongs to that school of ornithologists which believes in employing all available characters in classification, in ascertaining true affinities, to the end that the classification shall be a natural one and express as far as possible the real relationships of all existing families of birds, even to the minor divisions of species and varieties.

Within the past few years there have appeared some excellent summaries of classifications; for example, Ridgway's admirable presentation of the matter in his *Birds of North and Middle America*. "Nothing original is claimed for the classification here given," says its author, "except as to the form in which it is presented. It is simply the result of an elective process, the evidently good of other systems being retained and the obviously bad rejected, according to the author's ability to correctly interpret the evidence" (p. 6). In this connection I desire also to invite attention to the avian classification found in the *Catalogue of Osteological Specimens of the Museum of the Royal College of Surgeons of England* (Part III, Aves). This admirable piece of work is by Sharpe, who states that "The system of Classification followed in the present work is mainly that proposed by Henry Seebohm in his 'Classification of Birds,' and further elaborated in this 'Birds of the Japanese Empire.' There are some points in his system which I have slightly modified; but they are of minor importance when compared with the fact that every group of birds, as diagnosed by Seebohm, possesses a

combination of definite features, which are characteristic of the group, and of that group alone, be it Order or Suborder" (p. 1).

Finally, in many of the "Manuals" and "Keys" and "Handbooks" and "Check Lists" published in various countries, we have other classifications, but these, inasmuch as they do not enter upon the subject in its entirety, are apt to be more or less unsatisfactory and often misleading. The *Check-List of North American Birds*, prepared by a Committee of the American Ornithologists' Union" (Second and Revised Edition, 1895), is a very good example, for in it we find a classification that although it would be of great credit to a taxonomer of the Curvierian epoch, it certainly can now only be regarded in the light of a curious bit of antiquated literature which it would be difficult to fit into any modern taxonomy of the Class Aves published since the days of such worthy pioneers as Nitzsch, Illiger, and Müller. As cited above this classification appeared in 1895, yet in 1901 when Ridgway, who was a member of the aforesaid Committee responsible for the classification in the "A. O. U. Check-List," published his own taxonomic scheme the latter differed so markedly from the former that to compare them is quite like making a comparison of Wilson's old single-barrel, flint-lock gun with the finely finished modern double-barrelled, hammerless piece now in the hands of the present day ornithologist.

It would seem that we at least ought to be in position at the present time, or certainly in the very near future, to decide upon the main groups into which the Class Aves is naturally to be divided, yet such is by no means the case. This is the more remarkable, inasmuch as all the important part of the development of avian classification dates no further back than the one proposed by Huxley in 1867. This scheme belongs to the literature of the Darwinian epoch and was influenced by what was then known of the law of organic evolution, and consequently is the first scheme of classification worthy of our consideration. Huxley divided the Class into three orders, the Saururæ, the Ratitæ, and the Carinatæ, and these three orders were divided into their suborders and certain groups.

Seven years later, or in 1874, appeared the well-known classi-

fication of Garrod, who it may be said, almost entirely ignored Huxley's scheme by dividing the Class Aves into two subclasses — the first containing four orders and the latter three, or in other words two sub-classes and seven orders as compared with the latter's three. Garrod's initial scheme of classification is not thorough since we meet with such incongruities as the Cathartidæ being considered simply as a group in the same order with the Steganopodes, herons and others, while the Columbidæ and the Gallinæ are widely separated, and the penguins are placed as a family among the Anseres, immediately following the Anatidæ, or the ducks, geese, swans and their allies. Still keeping before us, however, the main divisions of the class it is to be noted that ornithologists had little more than fairly grasped the Garrodian idea of avian relationships when in 1880, six years after its publication, Sclater proposed another scheme. In it the Saururæ of Huxley are not considered, — the class is divided into two subclasses, the Carnatæ and Ratitæ, the former containing no fewer than twenty-three orders, and the latter three others, or twenty-six orders of birds, where Huxley only recognized three; and these three orders Newton considers to be so many subclasses, while he would divide the Ratitæ into no fewer than six orders. These classifications were almost immediately followed by Reichenow in 1882 who divided birds into seven main groups which he called series, and these seven series were represented by seventeen orders. It is very different indeed from any of the foregoing schemes and cannot be contrasted with them without great difficulty, while its chief interest lies in the fact that he published in connection with it a phylogenetic tree of the Class Aves, one of the first attempts of the kind employed in ornithological science.

Within the next ten years a number of important classifications followed, — all provisional schemes for the arrangement of the Class, but none the less entitled to our best consideration, coming as they have from the pens of the ablest living ornithologists.

Stejneger's appeared in 1885; Fürbringer's in 1888; Cope's in 1889; Seebohm's in 1890; Sharpe's in 1891; and Gadow's in 1892. Of all these Fürbringer's is the most elaborate and

exhaustive, being accompanied by several vertical aspects and horizontal projections of his phylogenetic tree. Indeed, the objection brought against Furbringer's classification, principally by Gadow, is that it is too long and too elaborate for practical use. I do not fully concur in this opinion ; moreover its author has, in many groups carried us a long way on the road toward determining the true relationships of birds and that, I take it, is the real goal we seek. In fact the converse of this would be an easy matter, that is to create a brief, artificial classification of birds based upon our present knowledge of the class, and adapted to the practical ends of the science. Any international congress of ornithologists, representatives from all parts of the world, could, in a few days, prepare such a scheme. But the problem is not to be settled in any such manner.

As it is we find hardly any more uniformity with respect to the schemes proposed by Stejneger, Fürbringer, Cope, Seebohm, Sharpe and Gadow, than is to be found among those of Huxley, Newton, Garrod, Forbes, Sclater, Reichenow, and others.

The majority of these schemes carry the classification down through the families, and, in special cases, in a few instances in each, through the sub-families. Huxley did not give the number of families in the Passeres, Garrod omitted the group entirely in his scheme ; Sclater enumerated thirty-one of them ; Reichenow but twenty-one ; Stejneger thirty-three ; Fürbringer reduced the typical Passeres to one single family, the Passeridæ ; in 1889 the present writer recognized twenty families of the North American Passeres, and Sharpe the following year practically adopting the scheme, included all the old world representatives, and by so doing admitted thirty-five families as making up the passerine group, — and so on.

There is little need of carrying such comparisons as these into the higher divisions into which birds have been divided. We would but meet with greater variance of opinions, made the more deplorable from the fact that the wealth of coinage in new names renders the comparisons instituted even more perplexing. Then this perplexity is in no way diminished when a taxonomer takes it into his head to incorporate all the known fossil forms of birds into his scheme, as quite a number have done, and, very properly so.

It may naturally be asked, what are some of the chief reasons why the classifiers of this group of vertebrates do not exhibit a greater unanimity — a fact more remarkable when we come to consider that a dozen or more of those classifications coming from the pens of competent ornithologists appeared all within a very few years of each other. It is certainly not due to the fact that it has been demonstrated that birds have arisen from a prehistoric and extremely ancient stock of animals in common with the Reptilia, for knowledge of this character ought to have the tendency to harmonize views and opinions rather than to introduce the element of disagreement among them. We may eliminate too, I think, any difficulty that has arisen from the discovery of the few fossil forms of birds we have come in possession of, for many of these belong to the minor groups of existing birds, while others are not calculated to disturb a natural classification. Indeed, in some instances, they shed light on the subject. Again, in that existing birds are so completely differentiated from all other classes of animals now living upon the surface of the earth, ought to make them the easier to classify. They alone possess feathers and this establishes a line of demarcation for them, standing between the group and the nearest mammals or reptiles, quite as clearly defined as the possession of a mainspring separates all modern watches from an hourglass. The problem then presents itself in this wise, — to ascertain the true relationships both near and remote existing among all living birds, and then prepare as simple a scheme as possible expressing these relationships in terms that shall be in harmony with the classification schemes adopted in the cases of other classes of animals. In doing this, one of the first difficulties to arise is the marked homogeneity of the group. It is like classifying so many thousands of black, leather-covered hand cameras; they all look a good deal alike on their outsides, and the task would be equally difficult were we not permitted to examine into their interiors and ascertain the differences in their other parts, as the different kinds of lenses, finders, shutters, and other contrivances. Exactly the same thing obtains with birds. The great variance of opinions in the premises at the outstart is due to the difference in the amount of knowledge possessed by the different classifiers, especially as

to the characters presented on the part of the insides of the objects they are attempting to classify, although in saying this I do not underrate the value of the external characters.

The facts, then, that birds are a very homogeneous group and the knowledge of all their characters possessed by individuals who have attempted to classify them, has differed very widely in amount, is the first factor that will account for the great differences to be seen in the various published classificatory schemes. These are not the only reasons, however, and another very obvious one is the attempt made by some classifiers to ignore the homogeneity of birds, and to arrange them after the manner of the other great groups of animals, such as mammals or fishes. In other words, the attempt is made to employ the same divisional groupings from subspecies to class in the case of birds, where perhaps no greater differences can be found than exist between a thrush and an ostrich, as they do in the case of mammals, where such gaps exist as the one separating man and the ornithorhynchus. The objection is raised here at once, however, that an order of birds, for example, is a very different thing from an order of mammals. This is a knotty question, and as time forbids my discussing it here, I can only say that it leads directly to another very obvious reason for the differences seen in the various arrangements that have been proposed for birds, and that is this: — although ornithologists, in this country at least, may be pretty well agreed as to what is meant by a species, it is not clear that the same apparent unanimity of opinion exists among them in regard to what is meant by a genus, or rather what constitute generic characters; and so on for families, suborders and other groups, until we arrive at the Class, and perhaps the Subclass, — groups, for evident reasons, again understood to possess the same value in all avian schemes of classification wherein they have been employed. The difficulty here is, no uniform laws have been drawn up setting forth for birds exactly what characters constitute specific characters, what generic characters, family characters, and so on up to Class characters. The consequence is that one avian classifier will employ subclasses in his scheme, which subclasses are designated in the scheme of another as super orders, or even as orders or some other divisional value in the scheme of a third

taxonomer, and so on for all those who have engaged in this difficult subject.

Finally, there is the great question upon which no two ornithologists now entertain similar opinions, and that is upon the various relationships of birds. Both this and the former question, however, depend entirely upon the amount of knowledge on the subject possessed by any particular taxonomer. The more exact and far-reaching this is, the nearer and sooner will he arrive at the truth.

In any event, it is very clear to me that the day is still far away when ornithologists will be agreed in reference to all these points. It is purely a matter of evolution, of development, and the acquirement of the necessary knowledge. Guess work will never attain the desired end, nor will any one man settle it. It seems to me, however, that we are in a position to discuss and settle one class of questions, that is in the case of birds, what groups shall be adopted in their classification, and what characters in birds themselves shall stand for those groups. For the rest the larger part of it depends upon substantially adding to our present knowledge of the morphology of these forms in its widest sense, and this to be supplemented by a very general knowledge of the entire life histories of all existing birds. From the very nature of things the latter advances with far greater rapidity than does the former, and we stand in great need of the addition of many more laborers in the fields of avian morphology. Death has materially thinned the ranks of this part of our army within a comparatively short space of time, and it has been principally the great captains of whom we have been deprived, — and we have by no means rallied from the loss of such workers in the anatomy of birds as Huxley, two of the Parkers, Gegenbaur, Garrod, Forbes, and other men of their calibre, power and influence, any one of whom would have said that the solution of the classification of birds lies in our commanding a knowledge of their history and structure.

New York City.

NOTES AND LITERATURE.

GENERAL BIOLOGY.

A Well Balanced Book on Theoretical Evolution.[1] — It seems to be generally agreed that we are beginning a new era in the study of Evolution; an era in which analytic and experimental methods will replace that of sharp logic. But the experimentalist works blindly without hypotheses and these the speculative writings have provided. It is a useful thing, at the beginning of this new era to have these hypotheses brought together by a broad-minded investigator; and this is the very arduous task that Plate has well done.

The immediate purpose of the work has been to stem the tide away from Darwinism, to show that whatever limitations the theory of natural selection may have as a complete theory of the origin of species it remains the only satisfactory theory of adaptation. The book, which is much increased in size over the first edition, is divided into five chapters. The first deals with the objections, less or more serious, that have been raised against Darwinism in the strict sense; the second with the different forms of selection and elimination; the third with the complementary theories; the fourth with the basic elements of evolution from which the theory of selection starts, namely, excess of births, variability, and means of isolation; the fifth with the range of applicability of the Darwinian and the Lamarckian factors. Then follow a Bibliography of over 10 pages and a good index.

The book is exceedingly satisfactory in most particulars. It is refreshing to find an author who does not insist that there is only *one* method of evolution. "Das Problem der Artbildung" he says, page 228, "darf nicht einseitig behandelt werden, weder ausschliesslick von Lamarck'schen noch vom selectionistischen Standpunkte; nur die Vereinigung beider Principien führt zum Ziele." Naturally the author does not follow Weismann in rejecting the inheritance of acquired characters and he is quite ready to accept the possibility of

[1] Plate, L. *Ueber die Bedentung des Darwin'schen Selectionsprincips und Probleme der Artbildung.* Zweite, vermehrte Auflage. Leipzig: Engelmann, 1903. 247 pp.

orthogenesis. In this breadth of view Plate doubtless approaches nearer to the spirit of the great master than the Neo-Darwinians. Nevertheless, in so far as a criticism may be aimed at the book it concerns Plate's unwillingness to accept more freely some of the other subsidiary or alternative theories that have been proposed. Thus the reviewer thinks that Plate does scant justice to the claims of the mutation theory; and in his discussion of means of isolation he entirely fails to mention Mendel's law of the segregation of parental qualities in the germ cells of mongrels. Nevertheless, this law must be an important factor in preventing the swamping of mutations. In his account of the different theories to explain organic adaptation there is not included the theory proposed by the reviewer and later by T. H. Morgan that there has been a selection by the organism of the environment for which its structure is fitted — but as the preface date is antecedent to the appearance of that theory such conclusion could hardly be expected.

This brief review can give no adequate idea of the scope, soundness and helpfulness of the book. It is recommended to biologists as by far the best on the subject.

C. B. D.

Experiments in Heredity.[1] — Stimulated by the rediscovery of Mendel's Law of crossing, Bateson and Saunders have thrown together the results of their studies on crossing plants and poultry. As this is the first extensive post-Mendelian account of hybridization experiments in animals it may fairly be called epoch-making.

Miss Saunders worked with two hairy species of Lychnis and also a glabrous variety; with two varieties of Atropa; two species, each with two varieties, of Datura; and various races of Matthiola. In the first cross the hairy character is dominant and the glabrous recessive, as shown by the fact that all the first crosses were hairy. In the second generation, however, both dominant and recessive forms appeared in Mendelian proportions.

The Atropa experiments were less complete, but appeared to be Mendelian, showing dominance in the first color of the type form. The Datura experiments, involving 12 characters, were much more complex. Also there were exceptions to Mendelism in some cases, although striking adherence to it in others. Finally, the Matthiola experiments were based on so many races mixed together that the

[1] Bateson, W. and Miss E. R. Saunders. *Report I to the Evolution Committee, Royal Society, London:* Harrison & Sons, St. Martin's Lane, 1902. 160 pp.

results are hard to follow ; some were clearly Mendelian, others clearly not ; and some of these aberrant cases seem to be examples of what Millardet has called "false hybridism" — where the second and subsequent filial generations show no trace of one of the parents.

The poultry experiments were made with Indian Game, White Leghorns, Brown Leghorns, White Dorking, and White Wyandotte. The pea comb and single comb when crossed followed Mendel's law, the pea being dominant. The extra (Dorking) and normal toe followed the law approximately, the extra toe being dominant. In other cases the results were non-Mendelian. Thus it may happen that when a usually dominant character is crossed with a pure recessive the first filial generation is not purely dominant, but a mixture of dominants and recessives. It appears that a usually recessive character may sometimes dominate. The mixed result in the first filial generation may also be due to the fact that the "dominant" used in the cross was not a pure bred dominant but gave off "recessive" gametes.

The last 35 pages of the work are devoted to an invaluable discussion of "The Facts of Heredity in the Light of Mendel's Discovery." Here some new terms are introduced. In experiments in hybridization two forms exhibiting antagonistic characters are crossed. There may be one pair or many pairs of these antagonistic qualities. The antagonistic qualities are called allelomorphs. The zygote produced by the union of gametes with allemorphs is called a *heterozygote* to distinguish if from a zygote formed of similar gametes (homozygote). Allelomorphs may be either simple like hairiness or smoothness; or they may be compound, as the variegated color of some flowers. When a compound allelomorph is crossed with a simple the second filial generation may show not two forms only but several — the compound allelomorph has broken up into its constituents.

The relation of Mendel's Law to "skipping a generation," to prepotency, to sex (since elaborated by Castle) and to Galton's Law are discussed. The whole work closes with an eloquent "outlook" over the future of experimental breeding.

C. B. D.

Walks in New England[1] is a series of lay sermons which appeared in the Springfield Republican a year or two ago ; they are the records

[1] Whiting, C. G. *Walks in New England*, with illustrations from photographs. London and New York, John Lane. 8vo., pp. 301, 24 illustrations.

of a saunterer among New England's woods and fields. They record the aspects of the changing seasons from March to December with eyes which, in turn, are those of a lover of plants and birds, a poet, and a deeply religious man. For science he cares little, as compared with "the intuition of spirit"; Emerson and Whitman are more to him than Darwin and Wallace. The letters are not full of accurate detail like Thoreau, nor of vivid coloring like Bolles; the style is often too involved and the thought too mystical to suggest comparison with Burroughs; but coming as they did from week to week, they must have been very welcome to many who could not share the author's rambles; they breathe the calmness, the toleration, the kindly sympathy of a true lover of out-door nature.

ZOÖLOGY.

Influence of Man on the Distribution of Reptiles and Mammals in Patagonia and Fuegia.— In a very complimentary review[1] of my recently published *Narrative of the Princeton Patagonia Expeditions*, Mr. Barnum Brown, who, as a representative of the American Museum of Natural History in New York accompanied me on my last expedition to that country remarks that my "observations on lizards should have been confined to that part of Patagonia north of the Rio Santa Cruz, for this river forms the natural southern boundary line for lizards as well as armadillos though a few have been scattered south of it by man." I have taken these small reptiles at Fitzroy's Springs on the north shore of the Gallegos river, at various points along the coast between Cape Fairweather and Coy Inlet, about the Salt lagoons at the estancia of Montes and Fernandez ten miles from Gallegos, at the Mount of Observation and at Greenwood's estancia sixty miles south of Santa Cruz and have observed them at many other favorable localities in the region south of the Santa Cruz River, while other travellers have reported them as being common not only in this region but on the *plains* of Fuegia as well. See Popper's account of Fuegia in Mulhall's *Hand-Book of the River Plate.* I see no good reason for attributing the present wide distribution of these lizards over the region south of the Santa Cruz River to the agency of man.

[1] *Amer. Nat.*, Nov. 1903, pp. 799–800.

Mr. Brown's remark that the presence of the guanaco in Fuegia while the deer, rhea and puma are absent from that island is attributable to the agency of man rather than to the superior powers of self-distribution possessed by the guanaco, may be correct, but the latter hypothesis seems to me the more reasonable one. If the presence of the guanaco in Fuegia is due to the agency of man, why is the rhea absent from that island? It is found quite as often in captivity among the Indians, could have been just as readily transported and is more prolific than the guanaco. The readiness with which the guanaco takes to water is well known in Patagonia as are also its powers of swimming and to these characters is due I believe its presence in Fuegia. The absence of the deer in Fuegia which, as is well known, is also a ready swimmer is I think due to the fact that it is a forest and mountain species and does not advance on the plains as far as the "narrows" of the Magellan Straits. Farther west the channels between Fuegia and the mainland are too wide to be successfully crossed by either the deer or guanaco.

J. B. HATCHER.

The Rat-tailed Rotifers.[1] — Jennings has published a most interesting and valuable monograph of the Rattulid Rotifers, which although a part of a series entitled "Rotatoria of the United States," actually includes the species of the whole world. In fact, one new species described (*Diurella dixon-nuttalli*) has never yet been found in America but only in England. The species are divided into two genera; *Diurella* in which the two caudal appendages or toes are equal or the shorter is more than a third the length of the longer, and *Rattulus*, in which these organs are more unequal, one being often quite rudimentary. The author states that these are not natural genera, but are justified by considerations of convenience. He remarks that the idea that all the species of a genus must be more related to each other than to any outside species has been largely given up in practice; but this might be admitted and yet it might remain true that the generic characters had not been acquired independently. If the more primitive *Diurella* type has given rise separately to two or more groups of species now included in *Rattulus*, it will be necessary to either divide *Rattulus* into as many genera, or unite *Diurella* and *Rattulus* under the latter (older) name. Of

[1] Jennings, H. S. A Monograph of the Rattulidæ. *Bulletin U. S. Fish Commission* for 1902 (1903). pp. 273–352. Pls. I–XV.

course it may be impossible to demonstrate this, in which case the present classification may very well be allowed to remain. The genus *Heterognathus*, Schmarda, is applicable to the species having the toes equal — part of the present *Diurella*. The author admits that this group may be thought worthy of separation, but he does not notice that the name belongs properly to a genus of fishes, the latter having five years' priority. If the equal-toed species deserve a generic name, a new one will have to be proposed.

Looking over the paper, one notices the absence of any records from the region west of the great plains, as well as from other great regions. It is to be hoped that students will arise in some of the neglected parts of the country, now that the study is made comparatively easy.

T. D. A. C.

Gardiner's Reports on the Fauna and Geography of the Maldive and Laccadive Archipelagoes have now begun a second volume. The First Part contains an account of the Alcyonaria, by Hickson and E. M. Pratt, of the nudibranchs by Sir Charles Eliot, of Sponge crabs by Borradaile, of Lagoon Deposits by Gardiner and on a Land Planarian by Laidlaw. The Part contains nine lithographed plates.

Hickson discusses the remarkable variability of the Alcyonaria and concludes that either they constitute a large number of closely similar species or else one species capable of extraordinary variation in circumstances that are approximately identical. For practical purposes the author regards those variations as species which are discontinuous. Hickson finds that the form and mode of branching are unreliable criteria of any species because they vary with accidental variations in environment and the presence of gall producing Crustacea that reside in the branches.

Eliot's Report contains many interesting general data, concerning swimming Hexabranchidæ, hidden but highly colored Dorididæ, self-mutilating Dicodoris, a Phyllid that secretes a liquid with disagreeable smell and others.

C. B. D.

Position of the Gordiacea. — Montgomery concludes[1] from a study of the adults that the Gordiacea agree with the Nematoda in only the tubular gmitalia and their opening into the cloaca. They

[1] *Zoolog. Jahrbücher* Abth. f. anat. xviii 1903.

agree with the Annelids in structure and innervation of the muscles and in dorso-ventral mesenteries bounded by epithelia. They differ from Annelids in entire absence of true metamerism, in the absence of a prestomial ganglion, in absence of seton and appendages and in structure of genitalia. The group cannot be regarded as degenerate Annelids (Vejdorvsky) or as modified Nematods, but must be considered as an isolated group (Funacher, von Siebold, Villot) until more details concerning the development are known. The pertinence of the peculiar genus *Nectoruma* to the group is at least questionable.

North Atlantic Invertebrata. — Several papers in the 1st Hefts of the *Bergens Museums Aarbog* for 1903 have an interest to students of the Invertebrata of our northeastern coast. Emily Amesen catalogues the Sponges of the Norwegian coast, the present paper containing the Halichondrina. R. C. Punnett enumerates the Nemertini of Norway in which thirty-four species are recognized, of which twelve are supposed to be new. Edward T. Browne reports upon a collection of nineteen species of Medusæ, mostly from the fiords around Bergen, four of them being new and eleven others not previously catalogued from Norway. Among the interesting points brought out is the fact that the peculiar sucking cups described by Hæckel in *Ptychogastria polaris* (*Pectyllis arctica* Hæckel) are only the stumps of broken off tentacles. Only four species of Leptomedusæ are enumerated in the collection. All three papers are well illustrated.

BOTANY.

The Desert Botanical Laboratory.[1] — Of the occurrences of recent date interesting to the botanists of this and other countries, one of great importance is the establishment, by the Carnegie Institution, of a laboratory at which desert plants can be studied in their native habitat. Messrs. Coville and MacDougal were asked to constitute themselves a committee of inquiry, to determine the most suitable place where such a laboratory might be located. We have before us

[1] Coville, F. V. and MacDougal, D. T. Desert Botanical Laboratory of the Carnegie Institution. pp. 1–58, Pl. I–XXIX, fig. in text 1–4. Publication No. 6, Carnegie Institution of Washington, Nov. 1903.

the report of their journey, undertaken early last year, which took them over most of the desert regions of the western part of this continent. The place decided on for the laboratory was a site about two miles from Tucson, Arizona, and since then the laboratory has been built and equipped. Besides the fact that the country around Tucson is of a distinctly desert type and the flora as varied as such a flora is apt to be, the practical questions of accessibility and of habitability were considered. With the two authors as advisory board, Dr. W. A. Cannon was appointed resident investigator and is at present engaged on various researches. Arrangements have also been made so that a limited number of trained investigators may avail themselves of the privileges of the laboratory. "Not the least important part of the duties of the resident investigator will be to aid visiting botanists and others."

This contribution besides containing a description of the trip undertaken for the purpose of selecting a site for the laboratory, also includes an account of the general botanical and climatic features of the deserts of the regions visited. While the two authors had both separately made trips to many of the same districts of the west, the itinerary of their present journey included almost all of the arid regions of the United States and of northern Mexico. Starting at El Paso they first made their way down to the sand dunes of Chihuahua, south of Samalayuca in Mexico. The winter vegetation of these siliceous sand hills is scanty, only a few forms are mentioned. The next point of attack was the Tularosa desert lying westward of Alamogordo, New Mexico, the most interesting feature of which is the region known as the White Sands, composed of drifting sand that is almost wholly gypsum. The characteristic plant of the dunes is *Rhus trilobata*, the roots of which bind the sand so effectually that clumps of the plant bring about the formation of pillars of sand when the surrounding dunes shift. A curious relation of plants of *Yucca radiosa* to the dunes was also noticed. Investigation showed that a Yucca growing out of the top of a thirty-foot dune, must penetrate with its trunk to the bottom. On excavating it appeared that the plant must have grown as the dune engulfed it. In the bottoms among the dunes the vegetation is much denser, a grass is plentiful and Ephedra is frequently met with.

Tucson was next visited, there the woody vegetation of the desert consists mainly of the creosote bush, the mesquite, joint pine, and several Cactus forms, while higher on the foot hills occur the giant Cereus, and species of the tree known as the palo verde. At the

time of the rains a variety of annual vegetation may spring up. From Tucson the authors proceeded to the Sonora region of Mexico, stopping at Nogales, and thence to Torres. Various interesting forms are described from this region, among the most remarkable of which is a cucurbitaceous tendril bearing plant, *Ibervillea sonorae*, whose root and stem base are enormously swollen for water storage, and a tree-like morning-glory (*Ipomoea arborescens*), which grows twenty to thirty feet high. At Guaymas on the Gulf of California, a curious mixture of plant forms was observed, the beach is lined with mangroves, while close to them were the strictly xerophytic Cacti, for as far as rainfall is concerned Guaymas is even more arid than Torres.

In the Colorado desert of California several types of vegetation are found, due to differences in the soils; there are the gravel hills, the alkali, and salt flats, the two last named showing a very restricted growth of vegetation. The fan-leaved palm, *Neowashingtonia filifera* is native to the eastern foot hills of the San Bernardino mountains which lie in the Colorado desert district. They grow in groves forming miniature oases where a clayey soil, from which oozes what water has come from the hills, crops out to the surface. Northward lies the Mohave desert where grows *Yucca arborescens* and *Juniperus californica*, while in the lower altitudes the creosote bush (Covillea tridentata), is the prevailing woody plant. From the Mohave the authors proceeded to the grand canyon of the Colorado, but were disappointed to find that the number of woody desert plants found along the canyon's sides were comparatively small. This they ascribe to the narrowness of the canyon which probably induces abnormal climatic conditions.

Following the account of the actual journey is a consideration of the characteristics of deserts in general and of North American deserts in particular. Meteorological tables are given, showing the rain-fall for various localities from Oregon, to San Luis Potosi in Mexico. One table of especial interest gives the mean annual precipitation as compared with the estimated annual evaporation. The ratio in favor of the evaporation is anywhere from 6 : 1 to 35.2 : 1. It is also pointed out that the distribution of rain-fall during the year is of great importance in determining the character of the flora. Another factor in the production of desert conditions which cannot be disregarded is the soil constituents, a fact that is illustrated by the conditions which exist in the gypsum containing White Sands of Tularosa, the "white alkali" which is mainly sodium sulphate and the "black alkali" where sodium chloride and sodium bicarbonate are the chief soluble constituents.

Historically the desert regions of North America are of interest, that area which was known as "the great American Desert" by cartographers as late as 1843, does not really exist as such. The deserts of this continent may be designated as the Sierra-Nevada desert, comprising portions of Utah, Idaho, Washington, Oregon, Nevada, California, Arizona, Baja California, Sonora, and Sinaloa; and the Chihuahua desert, which occupies the tableland of Mexico east of the Sierra Madre and north into Texas, Arizona, and New Mexico. It is further stated that for the purposes of this paper the desert lands of the Dakotas, of Montana and Wyoming may be considered as the extreme northern arm of the last named region.

As the closing section of the paper there is a discussion of the results of experiments by one of the authors, carried on at an earlier date. A comparison of two desert types, *Mentzelia pumila*, and an Artemisia, with two moisture loving forms, tomato and *Eucalyptus globosus*, shows that even in their natural habitats, where the conditions for transpiration are of course vastly in favor of the desert plants, the disparity between the water evaporation of the two is very great. As to temperature it was found that the plant-body of an Opuntia gave a maximum in the forenoon of as much as 111.2° Fahr., while in specimens of Cereus temperatures of 113° to 115° Fahr., were frequently found. The fact that this is above the critical temperature usually given for chlorophyll leads to the authors' suggestion that the protoplasm and the chloroplasts may have undergone changes which adapt them for such conditions, although, they add, it is not unlikely that the death of plants in such regions is as often the result of too great insolation as of lack of water.

The authors make no claim that their narrative is an exhaustive account of the regions visited, which considering the short time spent would of course be quite impossible, but express a hope that it will serve to show the great diversity which exists in the several floras which go to make up our desert flora as a whole. In this they can certainly feel that they have succeeded both in the text and in the admirable illustrations which are profusely scattered through the pamphlet. To any intending student of the conditions which exist in our deserts it is bound to be of great service and the full bibliography by W. A. Cannon which is appended will be an additional aid. This is the first publication relative to the desert laboratory, we may hope that many more will emanate from this source.

H. M. R.

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IN THEIR WIDEST SENSE

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THE ANATOMY OF THE NORTH AMERICAN CONIFERALES TOGETHER WITH CERTAIN EXOTIC SPECIES FROM JAPAN AND AUSTRALASIA.

(*Continued from page 273*).

D. P. PENHALLOW.

The Medullary Rays.

The medullary ray, in the various details of its structure as presented radially and tangentially, comprises some of the most important features for diagnostic and taxonomic purposes. While it presents numerous variations, these are, in the main, of such a nature as to give them very positive value for both generic and specific differentiations. Primarily the medullary rays are to be regarded as a residue of the original fundamental structure which has been left over in the genesis of the primary stele, but they are capable of reproduction or extension under the influence of the cambium in the course of secondary growth. In all such cases, however, they are typically composed of the same elements which are necessarily parenchymatous. Deviations from this structure may arise through the introduction of other elements, but such alterations always arise in a manner

which indicates their relation to the evolution of higher types of organization. The ray presents few features of value in the transverse section, and these will be sufficiently dealt with in the systematic portion[1] to make further reference to them at this time unnecessary. It only remains to point out that those rays in the Abietineæ which contain resin canals, and which present an unusual width, possess no special diagnostic value in this plane of section.

Radial Section.— Viewed radially, the medullary ray is seen

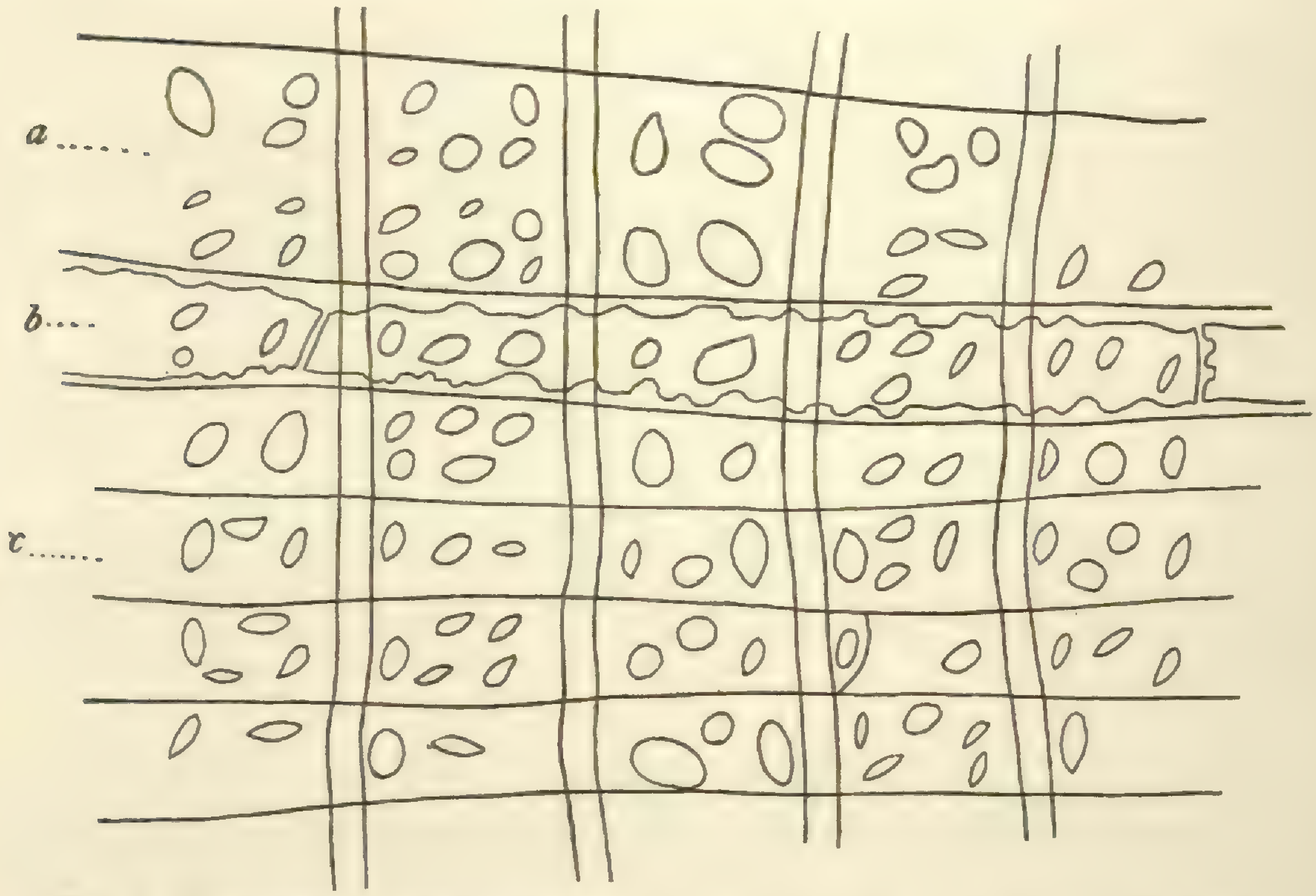

FIG. 17.— *Pinus palustris.* Radial section of a medullary ray showing characteristic pits on the lateral walls. *a*, a thin wall broken out; *b*, thick-walled parenchyma; and *c*, thin-walled parenchyma cells. × 280.

to be composed of a series of cells extended in a radial direction and superimposed so as to form a muriform band from one to many cells in height. In general terms, the higher the ray the lower the component elements, from which it follows that in one-celled rays the cells are usually highest; but this feature is only of general interest since it rarely has a bearing upon the chief questions at issue. In some cases two structural types may be

[1] The systematic portion here referred to, constituting Part II of the present series, will appear in the *Transactions of the Royal Society of Canada* for 1904.

recognized — the one containing resin passages, the other devoid of such structures. Where such passages occur the structure of the ray shows a variation of detail which makes it of no value for diagnostic purposes, and it is therefore eliminated from the following discussion.

A feature of primary importance in the constitution of the ray is the occurrence of two kinds of parenchyma cells. In 95% of the genera the upper and lower walls are always thickened by secondary growth and more or less strongly perforated by simple pits (Figs. 17*b*, 21 and 23). This feature also applies to 56.1% of the genus Pinus. It possesses no special value for either specific or generic differentiations except so far as it applies to cells which are markedly different and justify the special terms "thick-walled" and "thin-walled." It is obvious, then, that the thick-walled cell is to be regarded as the normal structure for the ray of the Coniferales as a whole, while the thin-walled represents the exceptional form which is introduced in response to some special demands. Although the thick-walled cells occur in the genus Pinus to the extent of 56%, they show a diminishing frequency, eventually becoming rare and ultimately replaced by thin-walled cells. Reference to them in the following diagnoses is always specified by (1). In 43.9% of the genus the upper and lower walls are thin and absolutely devoid of pits. For diagnostic purposes such cells are always referred to as (2). In some cases they are so undeveloped as to be obscure and readily broken out in the process of section cutting, so that they are often entirely wanting (Fig. 17 *a*). Such thin-walled cells are typically developed in *P. palustris*, *P. tæda*, etc., and it is to be observed that they are always associated with the highest forms of development. Transition forms occur. These are first seen in the soft pines where occasional thin-walled cells, devoid of pits, are interspersed and often coterminous with the thick-walled elements. In the hard pines the same relation exists, but it is gradually reversed until the thin-walled cells altogether predominate. Such gradations are exhibited in *P. coulteri*, *P. jeffreyi*, *P. pungens*, *P. tæda*, *P. cubensis* and *P. inops*, and they afford evidence of value as to the sequence in development of the species. In *P. murrayana*, *P. cubensis* and

P. insignis the transition forms exhibit much more detailed gradations by virtue of which it is often exceedingly difficult to distinguish between the two forms of cell, since whether coterminous or parallel the variations in thickness change in such a way that the one type passes gradually into the other. When these variations are viewed collectively and taken together with the general fact that the thin-walled cells are a feature of the higher types of organization, we may reasonably conclude that the thin-walled cells have been derived from the thick-walled through a process of arrested development. The cause of such alterations is to be sought for, and it will doubtless be found in connection with another component of the ray.

The terminal walls of the ray cells present three typical vari-

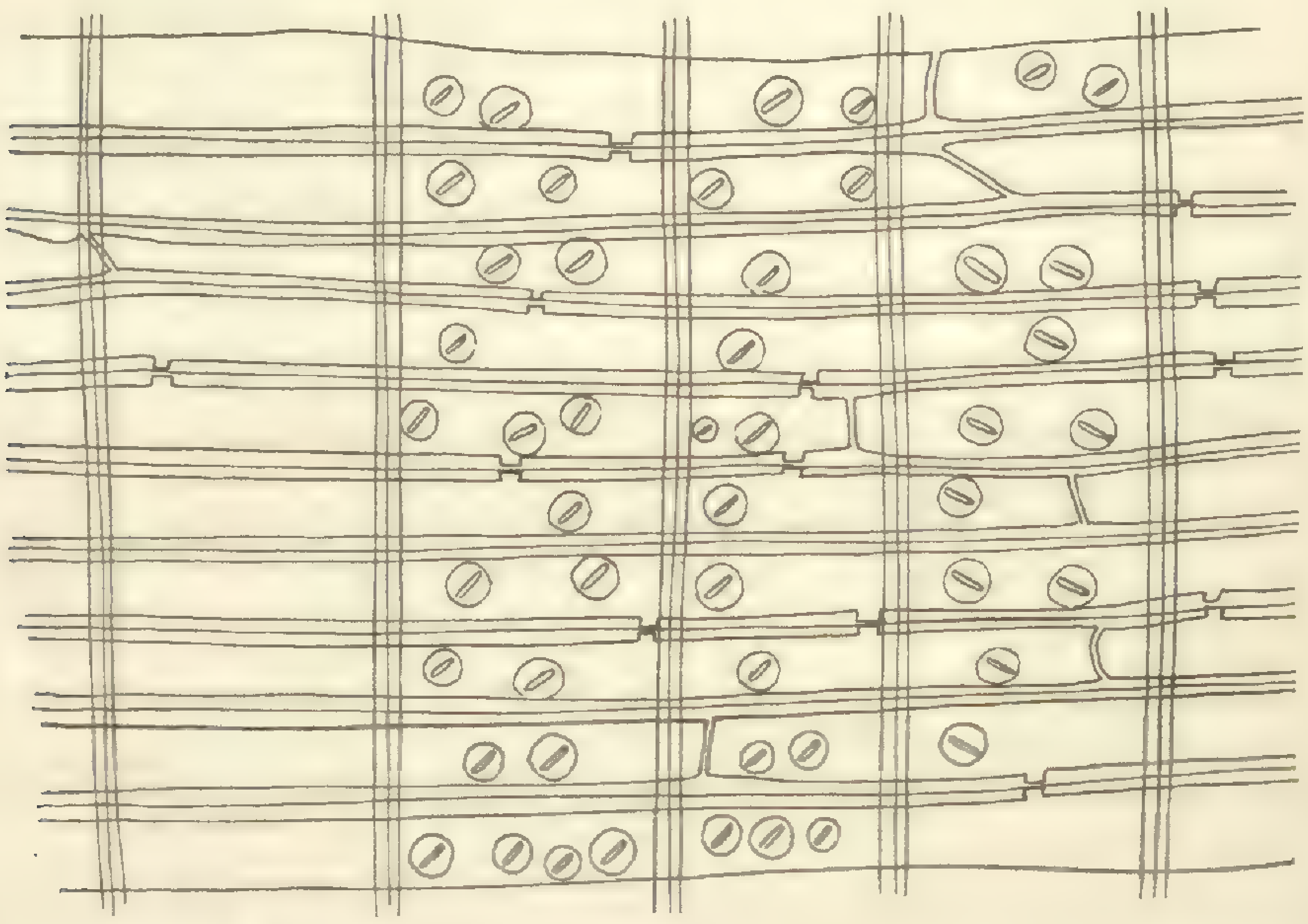

FIG. 18.—*Taxodium distichum.* Medullary ray showing the structure and position of the pits on the lateral walls; the straight ray cells and the thin, straight, terminal walls. × 280.

ations: (1) thin-walled and entire; (2) thin-walled and locally thickened, and (3) thick-walled and coarsely pitted (see table, D of anatomical data). The first feature is a characteristic of 52.6 % of all the genera, inclusive of Ginkgo, from Agathis to Sequoia, while it also appears in Cupressus and Abies in part as exceptional, and in the genus Pinus to the extent of 85.3 %. The wall presents no secondary growth in thickness, either locally or generally. In the majority of cases it crosses the line of the principal cell axis either at right angles or diagonally,

features which are usually of very secondary value, although in a few cases, as Taxodium, it may serve a useful purpose as an associated character, for differentiation from closely allied genera (Fig. 18). In other cases the wall is more or less strongly curved. This feature is prominent in Thuya, Cupressus, Podocarpus, Thujopsis and Cryptomeria, as also in the more highly developed hard pines. To a less extent it also occurs in Taxodium, and it constitutes a character of some value for differential purposes (Fig. 19).

The second variant differs from the first in that the otherwise thin wall is locally thickened (Fig. 20), the secondary growth forming one or more beaded enlargements. This is a feature which occurs exceptionally in Abies, Pseudotsuga, Picea and Pinus, but it is typical in Cupressus (66.0 %) and Juniperus

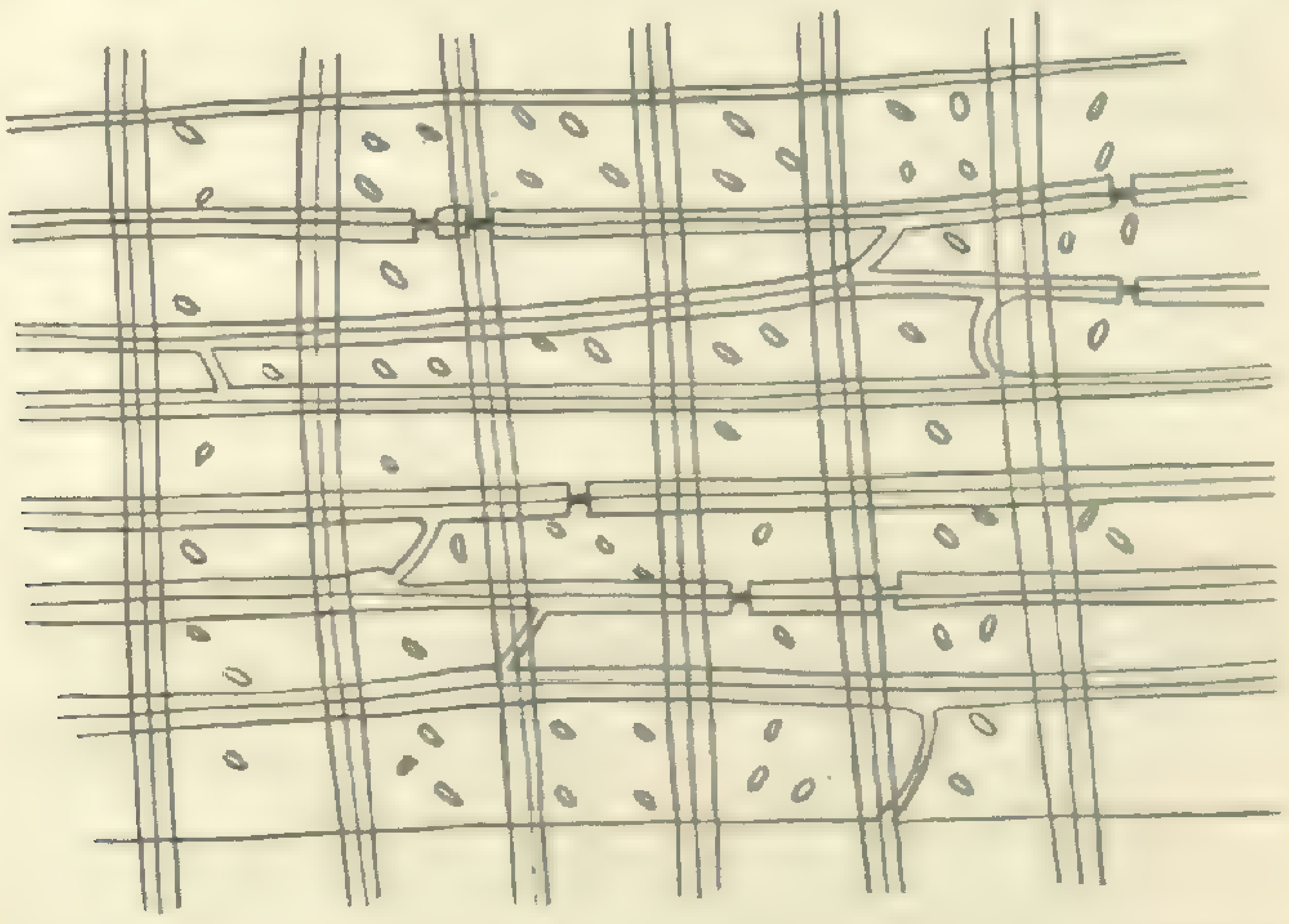

FIG. 19.—*Thuya gigantea.* Medullary ray showing the form and disposition of the pits on the lateral walls; the thin and curved terminal walls; the cells contracted at the ends. × 280.

(72.7 %) where it constitutes a diagnostic element of great value. It is in all cases, however, to be regarded as a transitional form between the first and the third variants, and from this point of view it also possesses a somewhat definite phylogenetic value. The third variant is characterized by a marked general, secondary growth of the wall, which thereby becomes more or less strongly thickened and traversed by numerous simple pits (Fig. 21). It occurs exceptionally in Juniperus and Pinus, but it is typical in Abies (90.9 %), Tsuga (100.0 %), Larix (100.0 %) and Picea (90.0 %). In Abies and Juniperus, where transitional forms sometimes occur, the walls in the spring wood may be

only locally thickened, but in such cases the typical feature always appears in the summer wood where such secondary alterations are most strongly emphasized.

For taxonomic purposes, such features possess a definite

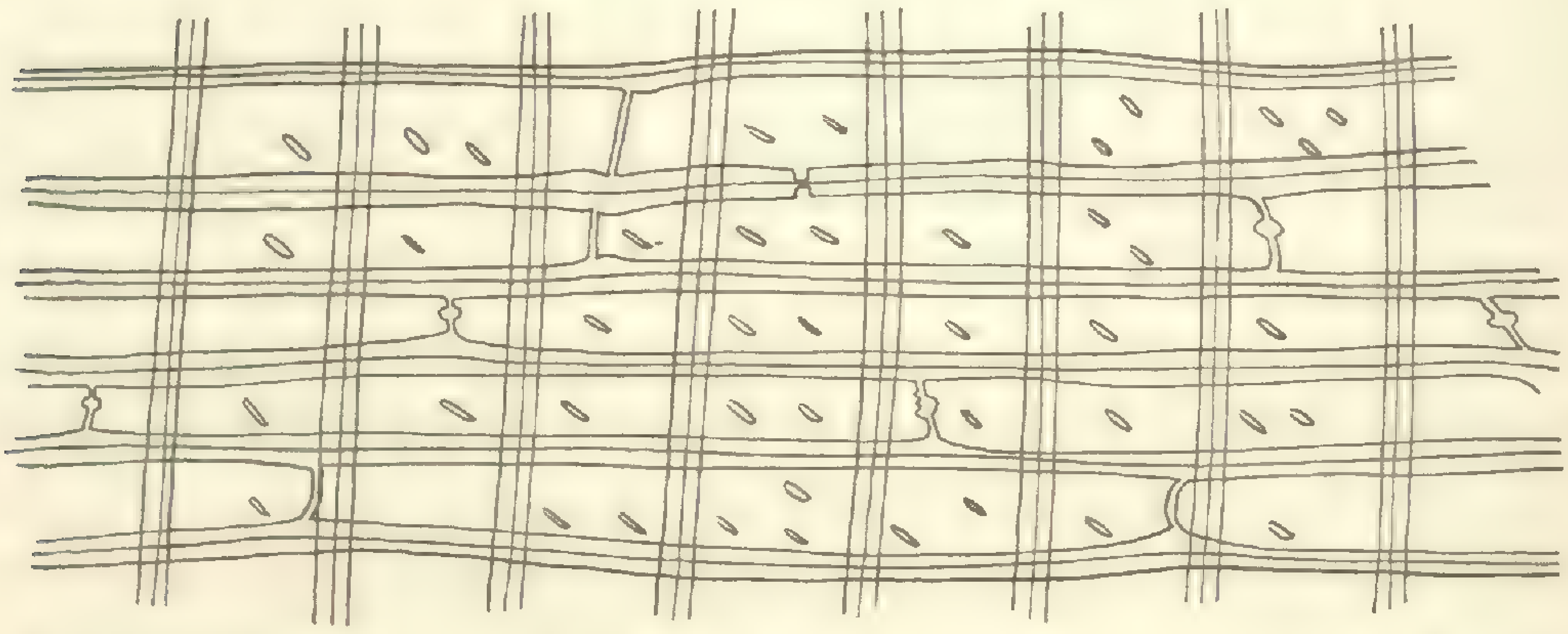

FIG. 20.—*Cupressus macnabiana.* Medullary ray showing the form and position of the pits; the thin, curved and locally thickened terminal walls. × 280.

value. The thick-walled cells of Tsuga, Larix and Picea permit of an easy and definite segregation of these three genera in those cases which otherwise might involve a strong element of doubt, and the same rule holds true, though to a less extent, with

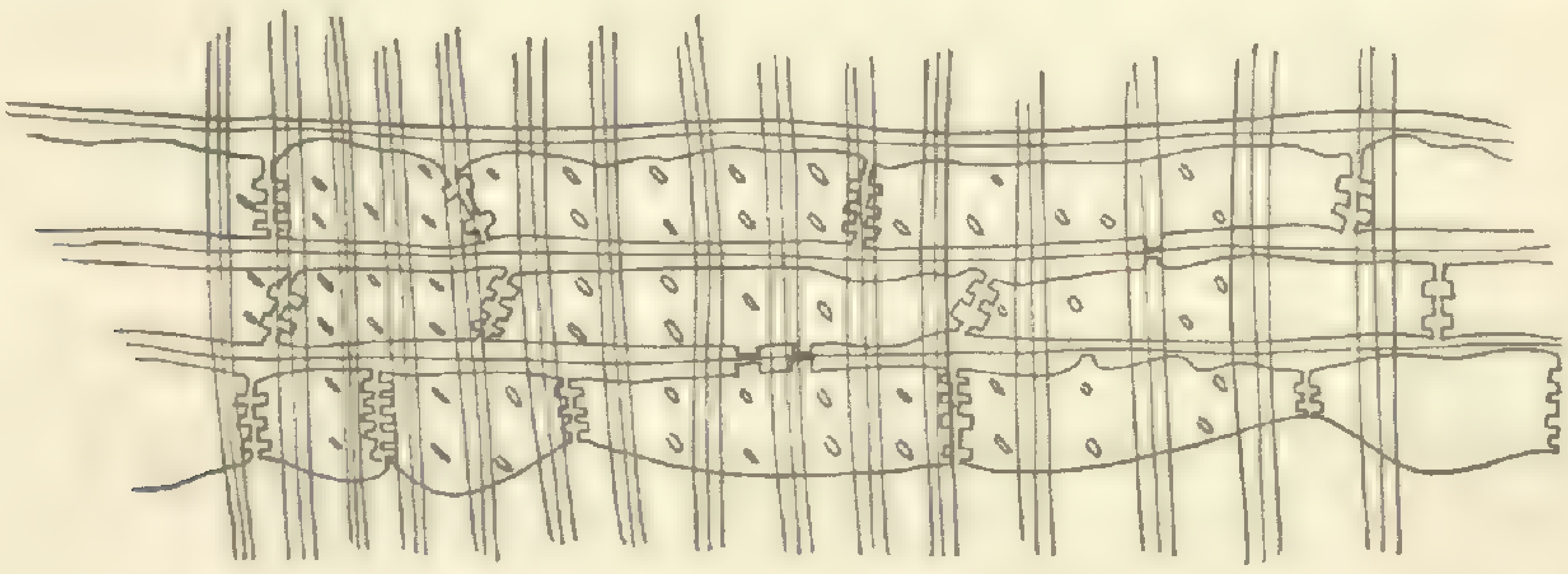

FIG. 21.—*Juniperus occidentalis.* Medullary ray showing the form and disposition of the pits on the lateral walls; the thick and coarsely pitted terminal walls. × 280.

respect to the locally thickened walls in Cupressus and related genera.

Pits on the lateral walls of the ray cells are an invariable feature of all investigated species of Ginkgoales and Coniferales, including fossil representatives and the Cordaitales. They vary very much in form, size and number. In such types as Juniperus, they are most diminutive (Fig. 21) and generally numerous, while in many of the pines, such as *P. resinosa*, *P. koraiensis* or *P. reflexa* (Fig. 22) they attain to maximum size and

occupy nearly the entire surface of the wall within the limits of a wood tracheid, thereby becoming few in number. In Sequoia (Fig. 23) or Taxodium (Fig. 18) they are typically oval; in *Pinus cubensis* or *P. tæda* (Fig. 24), they are variously lenticular, while in *P. resinosa* or *P. koraiensis* they are oval or oblong, or even quadrangular. Such variations as a whole, are far more

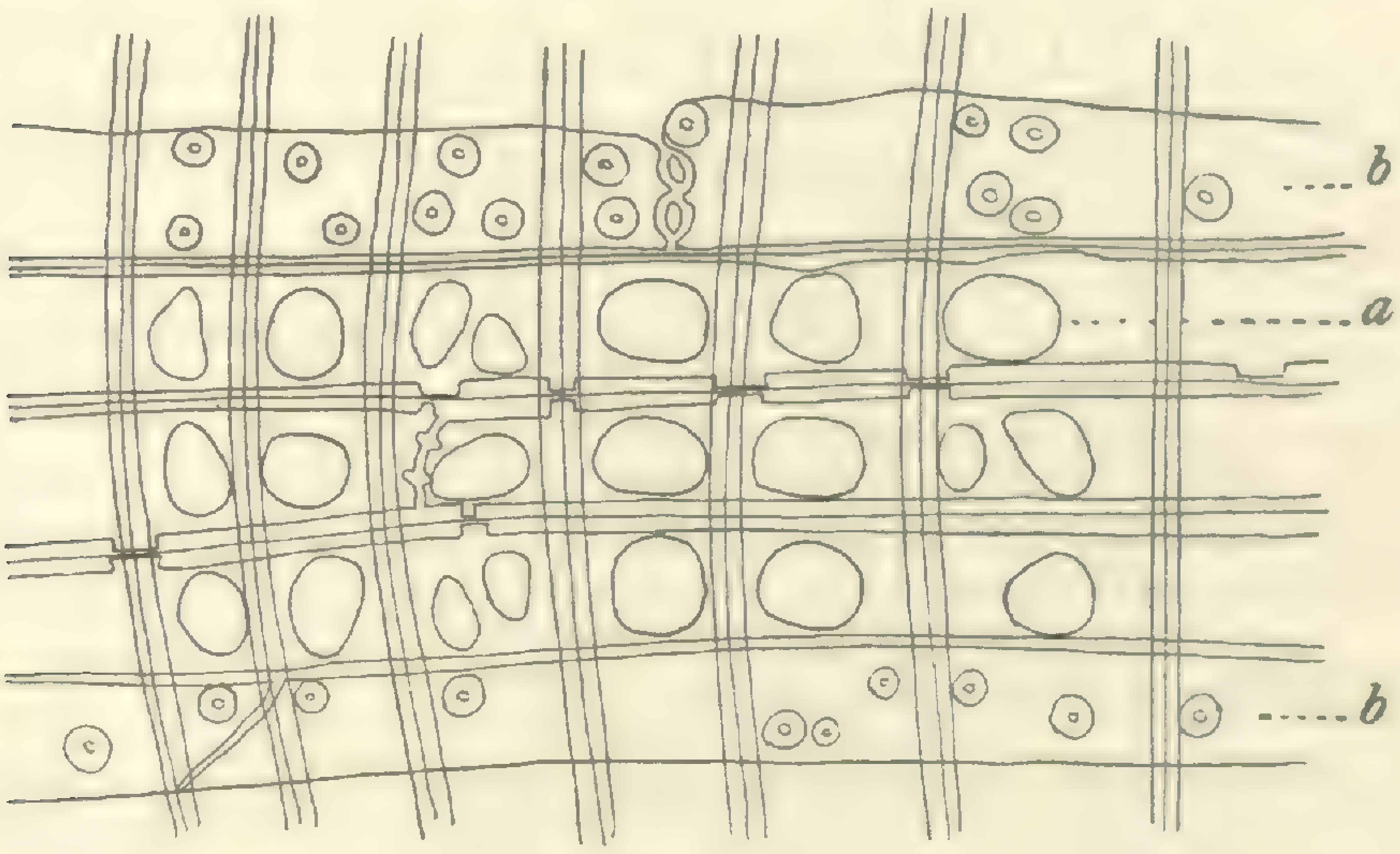

FIG. 22.—*Pinus reflexa*. Medullary ray showing (*a*) the form and disposition of the pits on the lateral walls; (*b*) the ray tracheids. × 280.

numerous and sharply defined in Pinus than in any other genus known. In all the investigated genera, the pit is bordered. This finds either partial or complete exceptions in the genus Pinus to the extent of 78.1 % of the species, in which the pits are either simple throughout, or they exhibit a more or less definite border in the summer wood only. That a border is a characteristic feature of fossil representatives, is justified by comparison with existing species, but it is not always recognizable in consequence of the alterations of structure due to the general process of petrifaction. Such obliteration not infrequently involves the pit orifice also. It is thus apparent that such structures often fail in the determination of fossils. In existing species the border is often so faintly defined as to be difficult of recognition, and this is especially the case in rays of a resinous character. In all such cases, however, the requirements of a correct diagnosis are fully met by the pit orifice. The general law of development then, is such that all genera except Pinus may be held to be characterized by bordered pits.

Their strong tendency to obliteration in that genus is found to coincide with the more marked development of ray tracheids which undoubtedly assume more completely the original functions of the parenchyma cells, these latter in consequence, suffering constant structural reduction, as in the hard pines.

In the distribution of the pits an important feature appears in

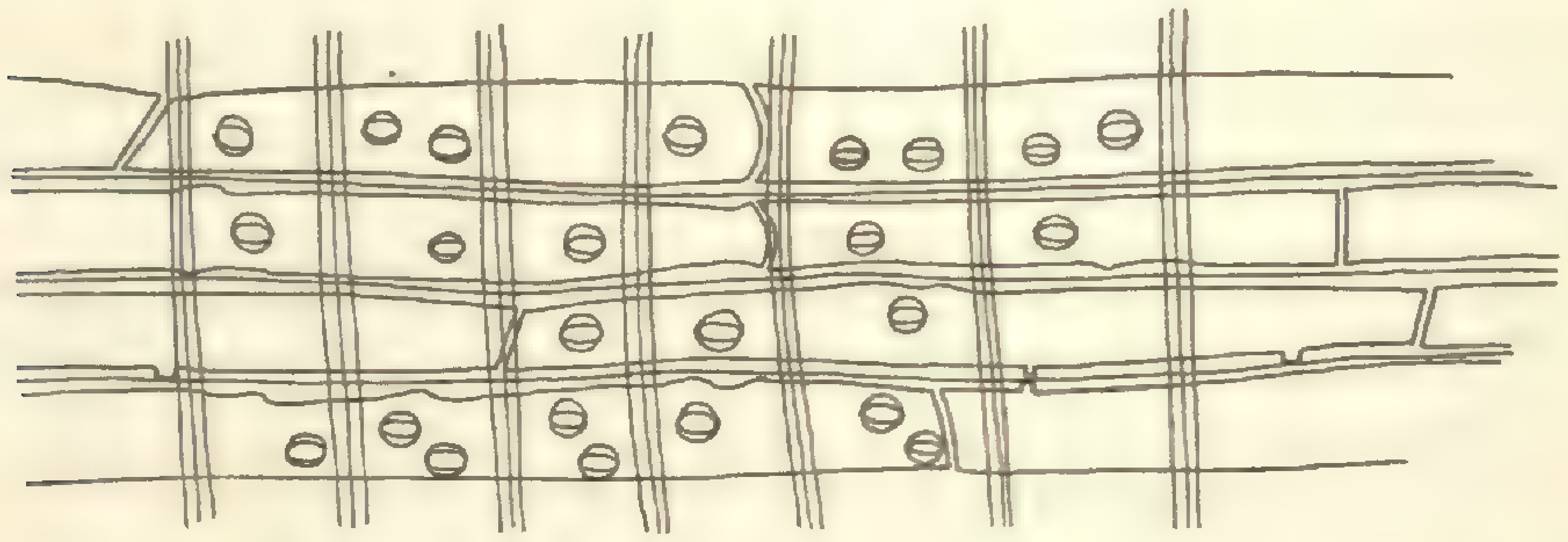

Fig. 23.—*Sequoia gigantea.* Medullary ray showing the form and disposition of the pits on the lateral walls. × 280.

the numerical variation in different parts of the ray. For diagnostic purposes it is necessary to have reference to the number of pits, not upon the entire surface of an individual cell, but within the limits of a spring or summer tracheid as the case may be. They are invariably most numerous in the region of the earliest spring tracheids, usually diminishing toward the summer wood where the change may sometimes take place abruptly, and in which they are most commonly reduced to one with occasional obliteration in the most highly modified tracheids last formed. A similar law of distribution is applicable within the vertical limits of the ray. When these structures are several cells in height, the number of pits is typical, and, within certain narrow limits, constant for all except the marginal cells. Thus if the normal number is 1–2 for the central cells, it may sometimes rise to 4, 6 or 8 in the marginal cells only, and such exceptions must be noted in diagnosis. When the ray is only one cell in height, the number of pits agrees with that for the marginal cells. Such numerical variations possess but little value for generic purposes, but as a specific character they may be held to constitute the principal differential feature in the last analysis. These relations are expressed typically in the genus Sequoia, the two species of which may be definitely differentiated. *S. gigantea* is characterized by oval and commonly narrowly

bordered pits, the broadly oblong orifice equal to the outer limits of the pit and chiefly parallel with the cell axis, 1–2, more rarely 3–4 per tracheid. In somewhat sharp and definite contrast to this, *S. sempervirens* has large, oval, narrowly bor-

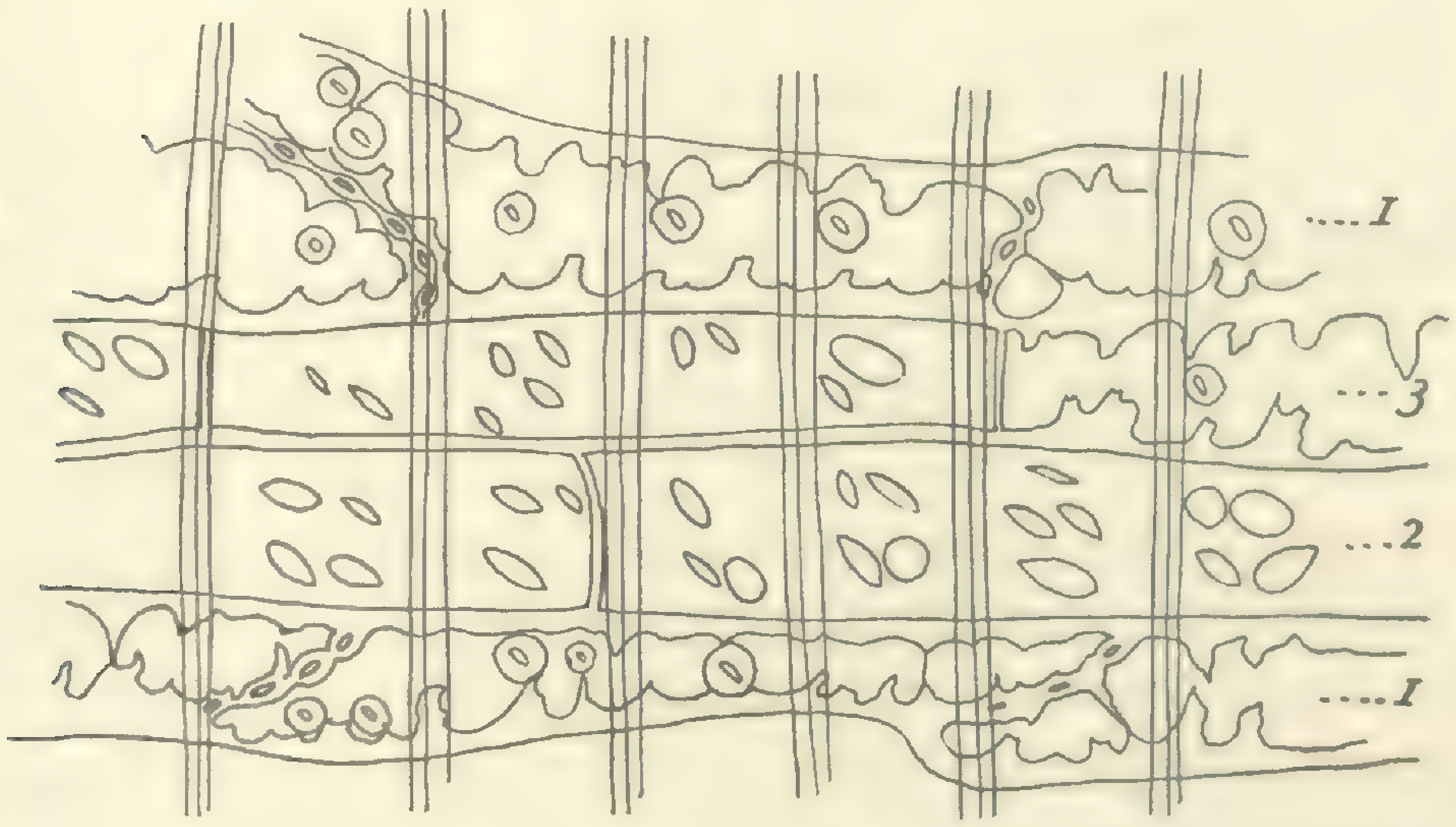

FIG. 24.—*Pinus serotina.* Medullary ray showing (*1*) the ray tracheids with dentate walls, (*2*) the structure of the parenchyma cells, (*3*) tracheids coterminous with parenchyma cells. × 280.

dered pits, 2–6 per tracheid, the round or broadly oblong orifice either parallel with or diagonal to the cell axis. In Libocedrus the pits are small, narrowly bordered, oval, with a lenticular, diagonal orifice, 1–4 per tracheid. Or again in *Larix americana*, the pits are "2–6 per tracheid becoming distinctly smaller toward the summer wood where they are abruptly reduced to 2, and finally 1 per tracheid." In *Cupressus pisifera* the pits are "chiefly 2 in radial series, or in the marginal cells and low rays upwards of 6 per tracheid." In *Taxodium distichum* the pits are round, conspicuously bordered and large, with a very narrowly lenticular and diagonal orifice which is often as long as the outer limits of the pit. But in the analytical key it will be observed that this genus is naturally brought into close relations with Sequoia which is also distinguished by large, bordered pits. The ultimate differentiation then rests upon the fact that in the latter, the pits are *oval*, the border often *narrow*, sometimes *obscure*, while the *olbong or* lenticular, usually rather broad orifice is generally parallel with the cell axis. As a final illustration the four pits of *Pinus monophylla*, or the 1–5 throughout,

finally reduced to 1–2 in the summer wood of *P. balfouriana*, point with much definiteness to these particular species, while among the hard pines the occurrence of large, oval or squarish pits, 1 or rarely 2 per tracheid, segregates a group of four species. Detailed as these features are, they are not accidental, but of such constancy as to admit of no hesitation in accepting the conclusions to which they point.

The length of the ray cell is subject to considerable variation, not only within the limits of an individual, but as between one species and another. Our studies, however, do not permit the formulation of a law applicable to specific differentiations, even if such a law does exist, which present evidence leads us to doubt; but details of length, in terms of spring tracheids, have been incorporated in all the diagnoses, since they are often very suggestive and thus may assist in the ultimate recognition of the species.

The form of the cell is of more evident value, although too much stress must not be laid upon it. The cell is either straight, as in Juniperus, Libocedrus or Picea (Fig. 21), or it becomes fusiform through contraction of the extremities as in Cupressus, Sequoia, Taxodium, etc. (Fig. 19). As a well defined differential character its value is only one degree higher than the length of the cell, and it has been introduced into the diagnoses for the same reason as a controlling factor of secondary importance.

In the higher Coniferæ the medullary ray is distinguished by the presence of an element which differs materially in its structure from the associated parenchyma cells. These elements have been designated by De Bary (9, pp. 491–492), as "ray tracheids." Their structure is so peculiar, and they present such important relations to classification and development, as to necessitate a somewhat detailed account of them, to some extent in recapitulation of well known observations by De Bary (9, p. 491) Hartig (19, p. 13) and Göppert (17).

As stated by De Bary, the ray tracheid resembles the parenchyma cells, from which they differ, however, in the presence of bordered pits on *all* their walls. Furthermore, such pits not only differ materially in form and size from the bordered pits of

adjacent parenchyma cells, but they are always much smaller than the pits of those wood tracheids on which they border. Such tracheids are invariable features of the ray in all the higher Coniferæ from Tsuga and Pseudotsuga to Pinus to the extent of 25% of the investigated genera. In Juniperus they occur very rarely, being found, so far as I am aware, in only one species (*J. nana*) out of a total of eleven, and they are so sparingly developed as to readily escape observation. In Thuya they are to be met with in *T. japonica*, likewise in a rudimentary state of development. Out of nine species of Cupressus they occur only in *C. nootkatensis*. Of the ten investigated species of Abies, they are found only in *A. balsamea*. In commenting upon this fact many years since, De Bary (9, p. 490), also pointed out that among European species *A. excelsa* is similarly exceptional, but no attempt has been made to interpret their significance. In Thuya, Cupressus and Abies the tracheids are strictly marginal in the composite rays, forming the entire structure in rays only one or two elements high. This relation obtains in all the higher Coniferæ in the first instance; but in Larix, Picea and Pinus, where there is a notable increase in numbers, they also become interspersed with the parenchyma cells and eventually predominate over them, a feature which is especially characteristic of the hard pines. Efforts have been made to show that in all such cases the two kinds of elements succeed one another in a definite order from above downward — or the reverse — but our studies have failed to show that this is capable of practical application to the purposes of classification, or even of phylogeny (9, p. 491). The great fact of importance for our present purpose, however, and one which stands out with much prominence, is that the ray tracheids are not a structural feature of the more primitive Coniferales, but only of the higher types such as Picea and Pinus. Furthermore, the primitive position for these structures is in the one or two-celled rays, or correspondingly in the margins of the composite rays.

In Thuya and Cupressus the tracheids appear to stand by themselves, and they exhibit no special relations to the parenchyma elements which would permit of inferences as to their possible origin. In the genus Pinus, on the other hand, where

the relations are somewhat complex, evidence does appear of such a nature as to suggest their derivation. In *Pinus inops*, *P. torreyana*, *P. pungens*, *P. clausa*, *P. tæda*, *P. palustris* and *P. cubensis*, we frequently find thick-walled parenchyma cells and characteristic ray tracheids coterminous with one another. This does not mean a simple association, since in nearly all such cases, as typically presented by *P. palustris*, they also show a graduated structure of such a nature as to confirm the belief that the one passes into the other by structural gradations. That such is the case cannot be doubted, and if further confirmation were needed it is afforded by the precisely parallel relations to be met with in the formation of resin cells and resin canals. A further fact of much significance from the standpoint of development, is that such interchangeable relations are peculiar to the highest types of the genus Pinus. But we may ask, what is the function of these structures which make their appearance only in the higher Coniferæ; what is the proper significance of their appearance there, and do any other plants offer parallel examples?

In the so-called medullary rays of *Lepidodendron selaginoides* (49, p. 141) there are numerous reticulated or spiral elements which are undoubtedly of the nature of tracheids, and they may be held to represent the ancestral form of the ray tracheids in the Coniferæ, toward which they bear the same relation that exists between the spiral protoxylem element and the characteristic wood tracheid with bordered pits. From this it is apparent that the ray tracheid of Pinus or Tsuga represents a primitive structure which reappears in response to conditions of growth and structural alterations of such a nature as to demand the interposition of more simple, because more primitive, elements for the proper performance of necessary functional activities. These activities, in the case of Lepidodendron, are probably expressed in the radial distribution of water (51, p. 141), and we are no doubt correct in assuming similar activities to be carried on in the higher Coniferæ. In all those species which present the primitive structure of the thin-walled ray cells, both fossil and recent, there are no tracheids to be found. As a tendency to thickening of the wall arises, there is also developed a sporadic

tendency to the development of ray tracheids as in Thuya and Cupressus. It is also a noteworthy fact that simultaneously with a general thickening of all the cell walls throughout the ray, as in the genus Tsuga, ray tracheids become a constant and prominent structural feature. This relation exists in Pseudotsuga, Larix, Picea and Pinus, and it is a remarkable fact that as the type of organization advances, and the structural modifications of the wall become more profound, the tracheids gain steadily in numbers and importance until they finally replace the parenchyma cells more or less completely. Such facts serve to direct attention to the idea that by such progressive alterations the ray cells gradually lose their normal functional powers with respect to the radial distribution of water, and under such circumstances it is imperatively demanded that this deficiency should be met through some other structures. Under these circumstances two alternatives are possible. First, that the thick-walled and useless cells should return to their primitive condition in opposition to the general course of development, and once more resume their appropriate functions. Such structural reductions do in reality occur in these very cases, as shown in *Pinus tæda*, etc., but it is to be observed that they are of the nature of a growth which has been arrested at such an early stage as to be devoid of many of the normal structural features. Furthermore, it would be difficult, if not impossible, to obtain evidence from other plants in support of a hypothesis of this nature. It is true that in the case of girdled pines the heart wood may resume an activity long since lost, and thus take upon itself once more the function of the sap wood, as also to some extent the function of the bark, but such renewed functional power does not in any way involve structural modifications of existing elements, and cases of this sort cannot be cited in support of the hypothesis stated. Under these circumstances, therefore, it is fair to conclude that such arrested development expresses diversion of energy to the preponderant tracheids.

The second alternative permits us to consider that in the ordinary course of development the ray cells gradually lose their functional activity as a result of extreme structural modification, and that this loss of power cannot be restored, even though the

wall may return to a primitive condition of structure through various phases of atrophy. In accordance with this idea the tracheid would be introduced as the most natural because the original medium for such activities as are centered in the ray, and it would therefore acquire additional importance both numerically and functionally in direct proportion to the loss of power experienced by the parenchyma cells. This appears to be a reasonable interpretation, and in the light of observed facts it would seem to be the correct one.

A structural feature of great importance in the ray tracheid appears in certain inequalities of the upper and lower walls which take the form of teeth-like projections into the cavity (Fig. 24). In what may be regarded as the most highly developed tracheids the teeth project across the cell cavity until they meet and coalesce, thereby forming a more or less definite reticulation which gives to the tracheid a very characteristic appearance. As seen in tangential section, such reticulations often appear as narrow bands crossing the cavity from side to side, thus giving the cell a varying aspect. Such dentate and reticulated tracheids are absolutely confined to the second section of the genus Pinus, in which they constitute one of the most characteristic features to the extent of 68.3 % of the species. A more detailed analysis of this feature, as applied to the hard pines, is desirable. In *P. resinosa* and *P. thunbergii*, the tracheids are simply dentate. In six species represented by *P. murrayana* the teeth extend into definite reticulations confined to the summer wood; but in six other species represented by *P. jeffreyi*, such reticulations are sparingly developed throughout the ray. In *P. tæda* a transitional form appears. Typically this species shows the tracheids to be sparingly reticulated, but occasionally they are strongly reticulated throughout. This brings to mind the further fact that in all species which are sparingly reticulated there is a marked tendency to strong reticulation in the summer wood. In the thirteen remaining species the tracheids are uniformly strongly reticulated throughout the extent of the ray, and this feature attains its highest expression in *P. palustris* and *P. cubensis*. It is therefore manifest that we have to deal here with a graduated development of such a

nature that the simply dentate tracheid is the most rudimentary, while the strongly reticulated is of the most advanced type of structure.

The value of the ray tracheid for taxonomic purposes depends upon: (1) its occurrence in certain genera, and (2) its structural peculiarities. The simple wall of the tracheid, in the great majority of cases, affords no basis of specific differentiation, but in the various forms of dentate and reticulated walls of the second section of Pinus, it is of well defined value in this respect. *Pinus resinosa*, *P. thunbergii* and *P. koraiensis* are all characterized by the occurrence of simple teeth which are sometimes sparingly developed. This feature is intimately associated with the occurrence of large, simple and single pits on the lateral walls of the ray cells. From this group *P. densiflora* may be differentiated by the reticulations in the tracheids of the summer wood. Among the hard pines, *P. tæda* is distinguished by ray tracheids which are typically sparingly reticulated throughout, but on the other hand, *P. palustris* and *P. cubensis*, which probably represent the highest types of the genus, are at once separated from all other species by reason of the extent to which reticulations are developed.

The relations which the tracheids bear to the parenchyma cells in the general composition of the ray also have an important bearing upon specific differentiations. In the genus Tsuga the tracheids are sometimes interspersed, affording the first instance of a relation which later becomes most prominent in the higher genera, and the same relation is also expressed in Pseudotsuga and Larix. In Picea there is a somewhat stronger tendency to an interspersal which is only expressed fully in Pinus. In the soft pines eleven out of thirteen species show, as a rule, as in the previous genera, that the tracheids are rarely interspersed, *P. aristata* forming a partial exception, as shown in a sparing interspersal. *P. monophylla* and *P. monticola*, on the other hand, show a strong interspersal of the tracheids, and in this respect they approach the hard pines. In the latter group we again find the first four species characterized by a rare interspersal. But passing on to the more highly developed species, such types as *P. clausa*, *P. palustris* and *P.*

glabra show that the interspersed tracheids are not only numerous, but that they eventually become conspicuously predominant and often constitute the bulk of the ray structure. It is evident then that such features possess an evident value for diagnostic purposes, particularly in the genus Pinus where the variations are numerous, well defined, and applicable to particular species or groups of species.

Tangential Section.— As displayed in tangential section, the medullary ray exhibits two principal forms, each of which presents features of great taxonomic and phylogenetic value. The type of structure which prevails, and which may be regarded as the fundamental form of the ray, is that of from one to many cells superimposed in a single series of varying height (Fig. 25). Such uniseriate rays are characteristic features of all the investigated recent genera. In 30 % of the genera, there is a sporadic tendency to a multiseriate form as expressed in the development of rays which are 2-seriate in part. Such enlargement is not confined to any particular portion of the structure, and within the limits of the same section it may arise at the centre or at either end. It is never found in Abies, Picea or Pinus, but it is met with in *Pseudotsuga macrocarpa*, three species of Cupressus, two of Juniperus, one each of Sequoia and Araucaria and two of Larix (Fig. 26). In Libocedrus such tendency is much more pronounced, and the rays may be described as 2–3-seriate in part.

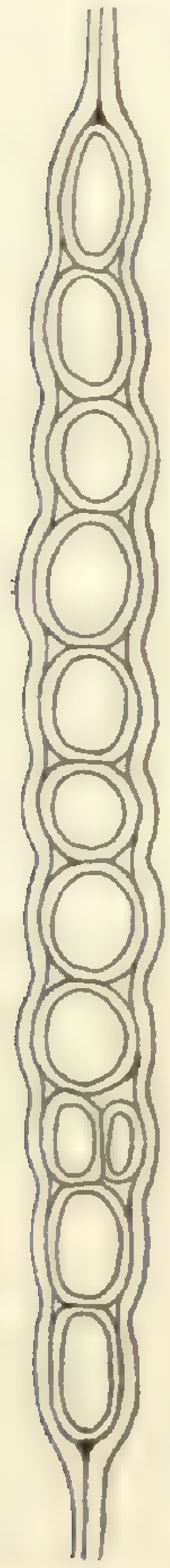

Fig. 25.—*Sequoia sempervirens.* Tangential section of a medullary ray showing a typically 1-seriate ray of broad form. × 280.

This feature is of so sporadic a nature that existing species afford no satisfactory evidence as to its origin or significance, but reference to Cordaites tends to throw some light upon this somewhat obscure problem. In fourteen species of Cordaites, three of which are European (25, p. 606–609) it is seen that the rays

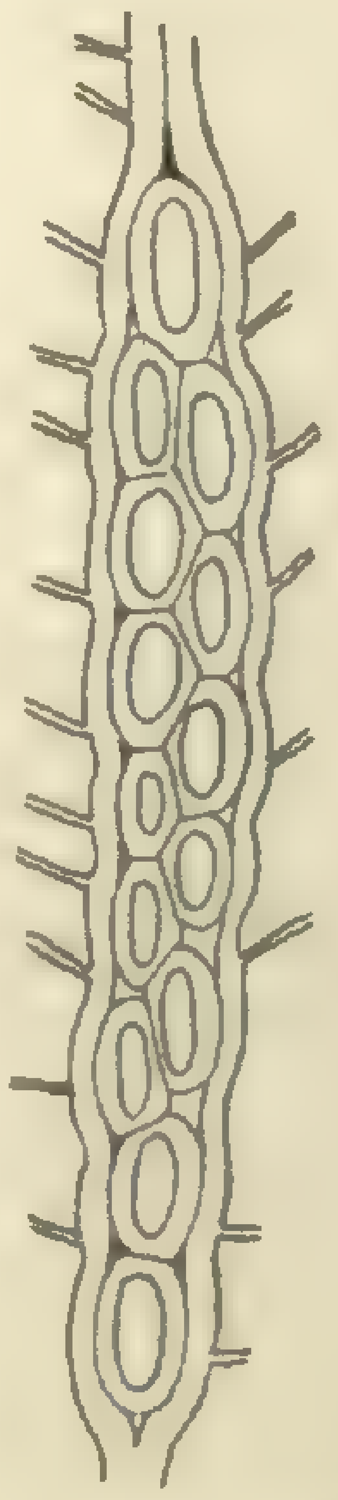

Fig. 26.—*Taxus brevifolia* Tangential view of a medullary ray, showing its 2-seriate character. × 280.

present four variants ranging from the strictly uniseriate form to 1–2-, rarely 3-seriate. The distribution is in the following percentage proportions:

1–2-, rarely 3-seriate	21.4 %
1–2-seriate	14.3 %
2-seriate in part	50.0 %
1-seriate	14.3 %

From this it would appear that Cordaites as a whole, approaches the primitive, multiseriate ray such as may be found in the Cycads, much more nearly than any of the existing species under consideration, and from this point of view it becomes possible to arrange a sequence showing the relative development in the following terms: (1) Cordaites, (2) Libocedrus, (3) all other genera as enumerated above. The evidence of fossil plants, however, shows that caution must be exercised in our estimate of what constitutes the primitive ray. The structure of Stigmaria shows a preponderance of uniseriate medullary rays (51, p. 224) and that such are primitive rays cannot well be doubted. In general, however, we are probably not far from correct in the assumption that the highest form of the ray is expressed in its uniseriate character. Deviations from this would then require to be interpreted as vestigial features which indicate a relatively lower type of organization in direct proportion to the increase of a tendency toward a multiseriate form.

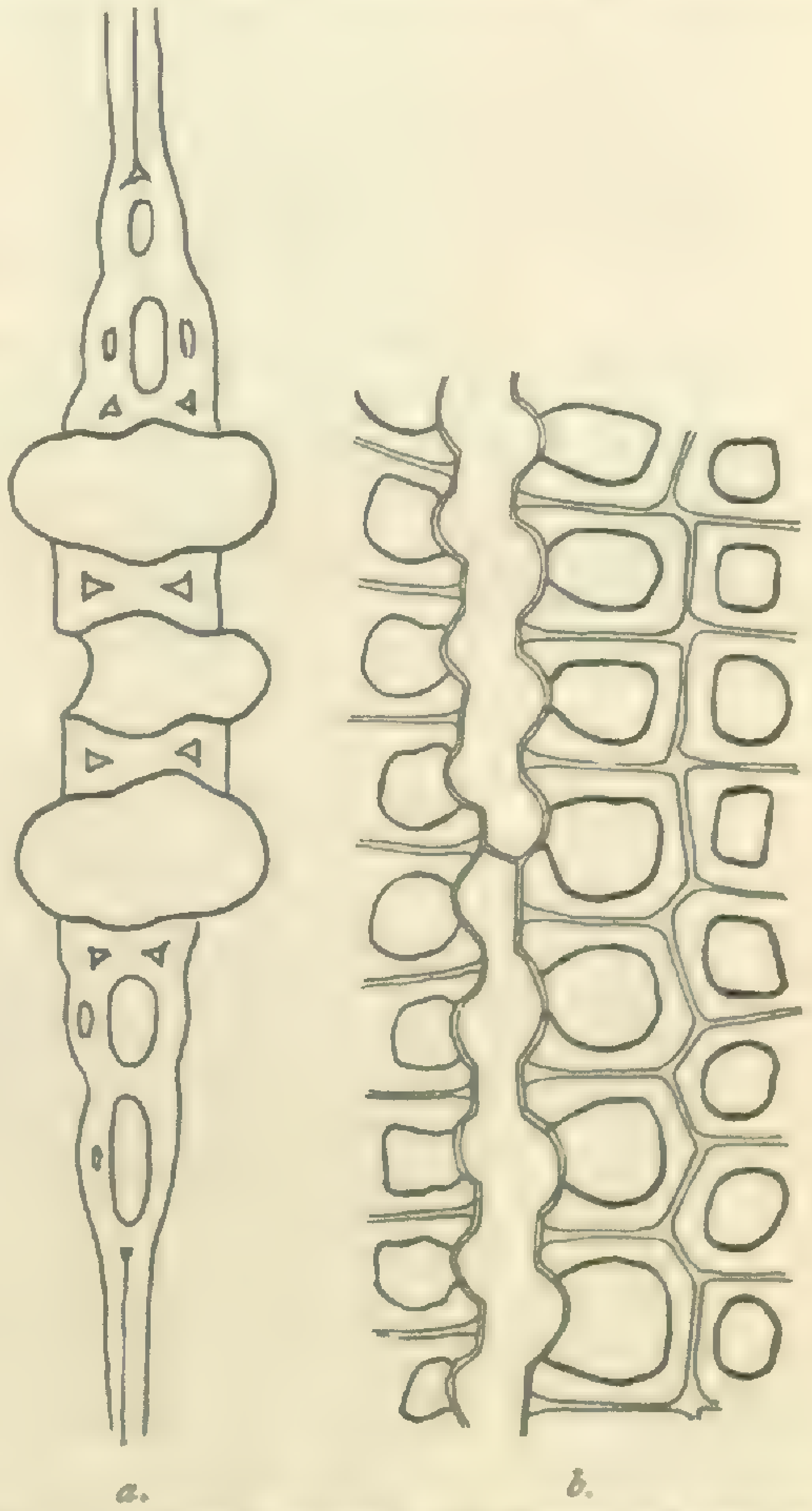

FIG. 27.—*Pinus reflexa.* (*a*) Tangential section of a medullary ray, showing the typically inflated cells. × 420. (*b*) Transverse section of a medullary ray, showing the inflation of the cells opposite tracheids. × 300.

In the majority of species, the side walls of the parenchyma

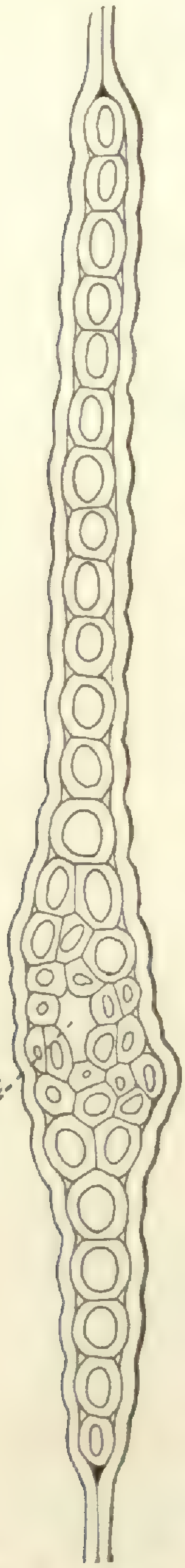

FIG. 28.—*Pseudotsuga douglasii.* Tangential section of a fusiform ray showing (*a*) the typical resin canal with thick-walled epithelium, but devoid of thyloses. × 280.

cells are thick and traversed by small pits. In the genus Pinus the wall is commonly thin and it closes the orifice of a very large pit on the wall of the adjacent wood tracheid. This is notably true of the soft pines in which the side wall either projects as a convex membrane, or it is concave and curves into the cell cavity. Such a feature is of very little if any importance with the exception *P. reflexa*, in which the thin side walls almost invariably project so as to give the cells a correspondingly inflated appearance (Fig. 27*a*). It is not only apparent in a tangential section, but it is very conspicuous in the transverse section (Fig. 27*b*) where the inflated walls are seen to project into the cavities of adjacent wood tracheids, thereby giving to the ray a beaded appearance. As an exceptional variation it possesses no apparent significance with respect to questions of descent.

The second form of the ray is that which has been designated as fusiform in reference to its characteristic outline (39). Such rays occur in relatively few of the existing genera to the extent of 20 %. They occur typically in Pseudotsuga, Larix, Picea and Pinus, and they are thus seen to be characteristic of the most advanced types. Among extinct species they are unknown except in the case of *Sequoia burgessii*[1] (41, 42–46) in which they present a remarkable exception to the general course of development and structure of that genus. The fusiform rays are peculiar in their structural features. They vary greatly in height as between different genera, and such variations also occur within a given genus, the extremes being met with in the genus Pinus, where *P. palustris* and *P. ponderosa* present the antithetic relations. In most cases they are much higher than the uniseriate rays with which they are asso-

[1] Dr. E. C. Jeffrey has recently discovered the same feature in another extinct Sequoia now in course of publication.

ciated, but this rule is subject to several exceptions. They are always distinguished by a broadening of the central tract by two to several times the original dimensions, thereby becoming more or less multiseriate. These variations depend upon the nature of the included structure which exhibits modifications directly related to progressive development of the genus. Such broadening arises abruptly in Pseudotsuga, Larix and Picea, so that the terminals above and below consist of a single series of cells with the general structure of the uniseriate ray (Fig. 28). In Pinus the broadening is less abrupt, diminishing in both directions somewhat gradually, thus giving rise to a region of lenticular form, which occupies upwards of half the height of the ray, or in some cases constitutes the entire structure. From this it follows that in such types as *P. palustris* (Fig. 29*b*), the terminals which are often prolonged to great length, may be linear and uniseriate, while in *P. clausa* the whole ray is lenticular in outline and the terminals consist of only one or two limiting tracheids (Fig. 30). Within the region of the central tract the cells are all thick-walled in Pseudotsuga, Larix and Picea, but in Pinus the cells are generally thin-

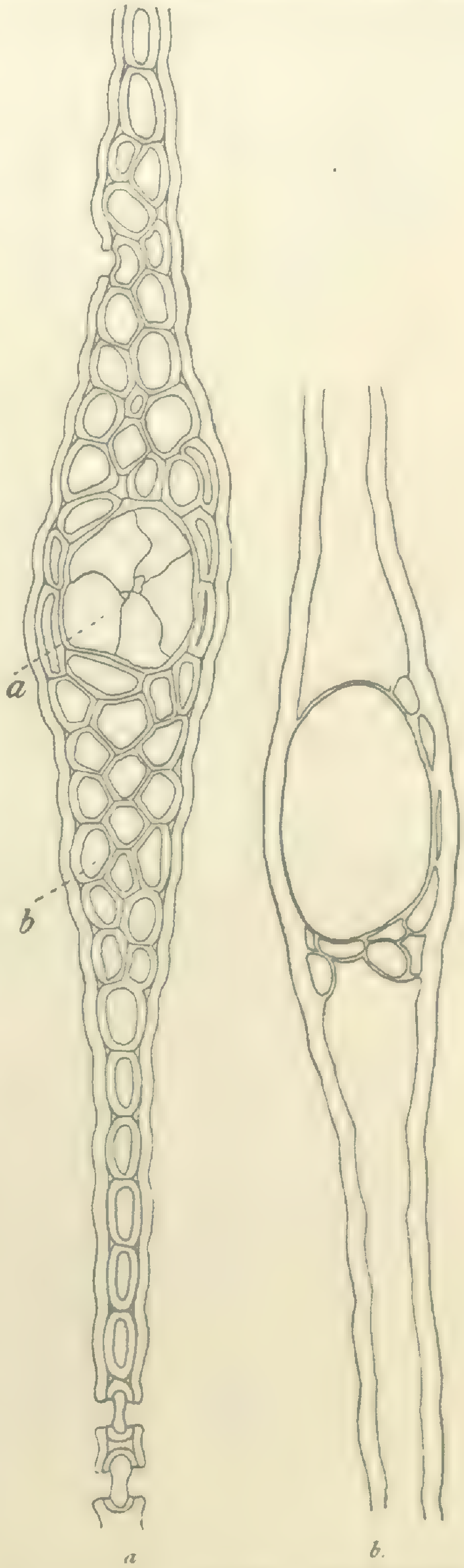

FIG. 29a.—*Pinus albicaulis.* Tangential section of a fusiform ray showing a typical resin canal with (*a*) thyloses, and (*b*) rather thick-walled parenchyma. × 280.

b.—*Pinus palustris.* Tangential section of a fusiform ray in part, showing thin-walled parenchyma broken out. × 280.

walled, and in the hard pines this feature is emphasized by a degeneration of the tissue to such an extent that it is readily broken out in making sections, whence it characteristically appears either much broken up or entirely wanting. The principal feature of such rays, and the one which determines their form, is the presence of a resin canal in each case. Such resin canals traverse the ray continuously for its entire length. They present the same details of structure as the resin canals which lie within the xylem. In Pseudotsuga, Larix and Picea, the central canal is narrow, especially in the first two genera, and the epithelium consists of a single layer of thick-walled cells. In Pseudotsuga and Larix (Fig. 28), thyloses are altogether wanting, but in Picea they are of sporadic occurrence. In Pinus (Figs. 29 and 30) on the contrary the canals are always distinguished by their great breadth; the epithelium is composed of one to several rows of thin-walled cells which are often resinous and often much disorganized, while thyloses are an invariable feature of the central canal.

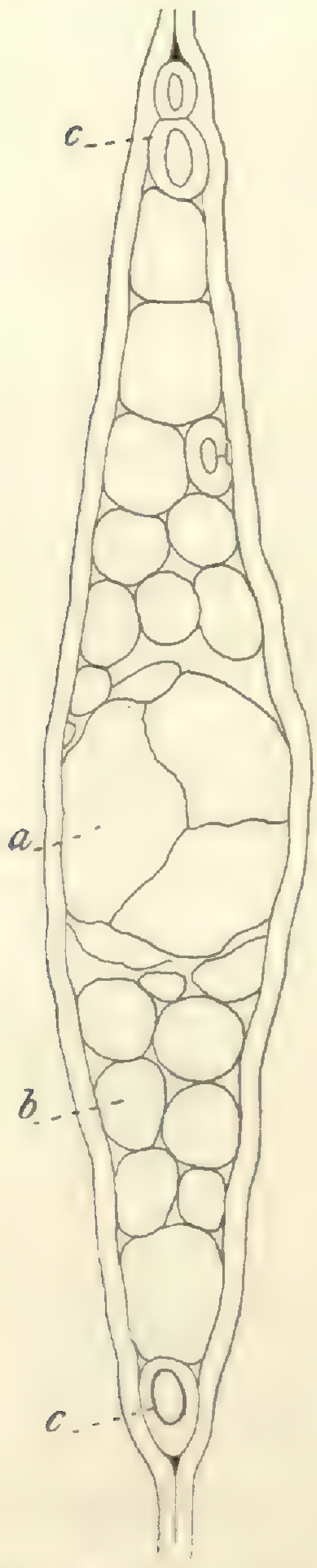

FIG. 30.—*Pinus clausa.* Fusiform ray showing (*a*) the resin canal with thyloses, (*b*) thin-walled parenchyma cells and (*c*) the terminals composed of only one or two tracheids. × 280.

A comparison of different genera and species shows that there is a somewhat striking variation in the number of uniseriate rays (tangential) to a given area of section. Such variations may arise within narrow limits in the same species according to location and conditions of growth, but apart from this there are somewhat constant variations between different species which may be expressed by the use of the relative terms few, many. No attempt has been made to define such variations and more exactly, but it is quite possible that a determination of the average number to a square centimeter, or other convenient unit, might disclose a somewhat greater differ-

ential value than is at present apparent. A simple illustration will serve to afford an idea of the rather limited specific value of this character. In *Taxus cuspidata* the rays are numerous, while in the two remaining species they are relatively few. The same feature applies to the differentiation of *Torreya nucifera* from the other species of that genus. In *Pinus clausa*, *P. serotina*, *P. murrayana*, etc., the same rule applies, but in all such cases it cannot be accepted as final.

The height of the ray is subject to such variations, even within the same species, that it cannot be defined with sufficient accuracy to admit of its application to classification in more than a very general sense. It is true that the rays of Ginkgo are always low, while those of Taxus and Torreya are often high. In Juniperus they are commonly low, while in Pinus they range from low to very high. Such variations do not possess sufficient constancy to admit of either generic or specific application in the strict sense, though they not infrequently serve a useful purpose as controlling factors, and they are therefore incorporated in all the diagnoses. Variations in breadth have a much more definite value, since the element of constancy is well defined. The genus Thuya (Fig. 31) may almost invariably be differentiated by this feature. In Cupressus, *C. thyoides* may be distinguished by a similar feature, while *C. arizonica* and *C. goveniana* are equally well indicated by the great breadth of the rays. The same rule applies also to Juniperus, Sequoia (Fig. 25), Pinus, and other genera, whence it appears that this feature is of specific value. It is always associated with and dependent upon the form of the component cells (tangential) which afford a means of distinguishing genera and species with much directness. The narrowly oblong cells of Thuya (Fig. 31) serve to separate this genus without difficulty, since a similar feature occurs but rarely elsewhere, and then in such association as to make the differentiation clear. In Juniperus the genus is separable into

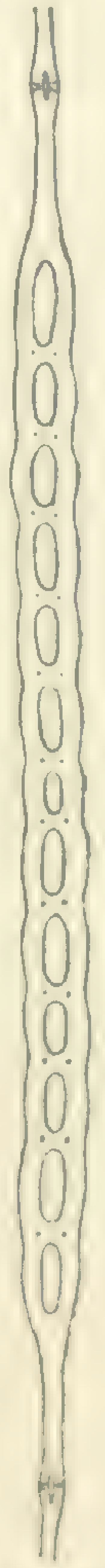

FIG. 31.—*Thuya gigantea*. Tangential section of a ray, showing the typically narrow and oblong cells. × 280.

four well marked divisions: (1) round to oval or transversely oval; (2) rays broad, the cells oval to round, chiefly round; (3) chiefly oval, and (4) rays narrow, the cells oblong to oval, chiefly oblong. The broadly oval and thin-walled cells of Sequoia separate it from associated genera. In Picea the genus may be subdivided accordingly as the cells are (1) variable, round, oval or oblong; (2) equal and uniform, oblong or oval.[1] Capressus is similarly separable into groups. But more specifically it is not difficult to separate *C. arizonica* and *C. goveniana* by reason of their broad rays and very conspicuously transversely oval cells, from *C. pisifera* with its round or oval cells and *C. thyoides* with its narrow, oblong, rarely oval cells. In the genus Pinus attention is at once directed to *P. murrayana* by the conspicuously round or transversely oval, very unequal and variable cells.

The interspersal of the tracheids often imparts a characteristic appearance to the tangential aspect of the ray, especially in the genus Pinus, and more particularly among the hard pines. In this group the tracheids present very variable forms and sizes. In such types as *P. glabra* they are small, oval or round, and wherever they occur they give rise to a marked local contraction. In *P. palustris* and *P. cubensis* they are commonly oblong and not infrequently they become several times higher than broad. As they are almost invariably narrower than the associated parenchyma cells, they cause a local contraction which sometimes extends over considerable distances. In *P. palustris* the predominance of the tracheids is carried so far that the rays are chiefly composed of them, and it then becomes appropriate to apply the term interspersed to the few parenchyma cells. In all of the more highly organized rays of the hard pines the appearance of the structure is so complex and variable that a proper diagnosis can be drawn only when we take cognizance of the principal aspects presented, and these sometimes amount to as many as four in number.

A consideration of the various structural features thus discussed in their relations to classification will show that no other

[1] The term equal here applies to cells of the same ray which are of the same width; uniform to the cells of all rays which are pretty constantly of one form; the contrasting terms being unequal and variable respectively.

portion of the stem possesses so many elements of importance as the medullary ray which, in consequence, attains the highest value in this respect and affords differential characters of wide range, great prominence, easy recognition and of primary importance in the differentiation of groups, genera and species; and as a general summary, the utility of these characters for such purposes is approximately indicated in the following tabulation:

1 Rays (tangential) of two kinds.
2 Ray tracheids.
3 Pits on the lateral walls of the ray cells simple or bordered.
4 Terminal walls of the ray cells thin and entire or locally thickened. } Generic. (1–7)
5 Form and character of the ray cell (tang.)
6 Form and size of pits on the lateral walls of ray cells.
7 Ray tracheids dentate or reticulated.
8 Direction and form of orifice of pits on the lateral walls of ray cells. } Specific. (5–12)
9 Upper and lower walls of ray cells.
10 Ray tracheids interspersed or marginal.
11 Disposition of pits (radial).
12 The number of pits per tracheid.

The Relations of Medullary Rays to Development.

We are now in a position to determine the relations in which the various structural features of the medullary ray stand to development, and for this purpose it may be most convenient to discuss them in that sequence which is apparently consonant with the general order of evolution of the entire group.

It has been ascertained that bordered pits are characteristic features of the lateral walls of the ray cell in 72.4 % of the investigated species, and that in the remaining 27.6 % among the higher types, simple pits predominate, but a closer scrutiny of this latter group discloses some features of more than passing

interest. Reference to the table of anatomical data will show that the change from bordered to simple pits is entirely confined to the genus Pinus, and that it does not rise abruptly as if in response to some unusual condition whereby a profound alteration in the usual course of development was induced; but it is effected by stages, showing that whatever influences were brought to bear, they operated gradually through a somewhat prolonged period of development, while here and there strong tendencies to reversion were manifested, and that the alteration was finally effected in a permanent way, only in the most highly developed pines. Commencing with *P. lambertiana* it will be observed that some species of the soft pines are characterized by simple pits. Among the hard pines *P. clausa* and *P. rigida* have bordered pits, while the six following species again show simple pits. We next come to a group of four species, with one exception (*P. murrayana*) Japanese, in which there is a mingling of both bordered and simple pits, showing a decided persistency of the primitive character in the face of conditions which involve a change. Following these are two species with simple pits, one with transitional features, five with simple pits, one with bordered pits, one with the transitional form and the remaining six species with simple pits, only. It will therefore be seen that these changes occur in waves, and that within the limits of forty-one species there are three complete and six incomplete recurrent phases. If we were arguing from purely theoretical grounds, all of these species should be arranged in such order as to show, (1) bordered pits, (2) transitional forms and (3) wholly simple pits, and we should thereby gain a perfect, developmental sequence. But such a position would not be justified by other evidence of an equally, if not more weighty character, and it is our object to interpret the facts as they are found. It has already been shown that the occurrence of simple pits in the pines is consonant with a higher type of development, and that the change is not only accompanied by sporadic reversions or survivals as one may choose to regard them, but that the change as a whole is a process of reduction. From this point of view then, we must regard the occurrence of bordered pits in *P. clausa*, *P. rigida* and *P. pungens* as pure survivals of a more

primitive structure, a feature which is less perfectly expressed in such transitional forms as *P. koraiensis* or *P. inops*. But a mere mingling of the two kinds of pits in the same species is not the only evidence in this direction. The mingling of simple and bordered pits does not occur indiscriminately, but in accordance with a well defined law to the effect that the former are characteristic of the spring wood throughout its entire extent, while the latter occur only in the summer wood where they might be expected if at all, since the arrested development which might be complete in the case of relatively thin-walled cells, could be readily overcome in part, in walls of greater secondary growth. This in no way conflicts with the observed fact that in the majority of cases, the usual course of development is such that the bordered pits of the spring wood very commonly become reduced to simple pits in the summer wood in accordance with De Bary's law as already stated in application to other cases. Constancy in the structure of such pits has been found to be characteristic of Cordaites, Ginkgo, the Taxaceæ and all the lower forms of the Coniferæ, from which we may conclude that the bordered pit is essentially a primitive character. On the other hand variation is a well marked feature of the pit in the genus Pinus as first expressed in the large, oval or squarish and open pits of *P. resinosa* or *P. thunbergii*, and as later appears with greater frequency in the smaller and very inconstant pits of *P. tæda* or *P. palustris*. Such variations then, involving a gradual and complete transformation to the condition of simple pits, are characteristic only of the more highly developed pines, from which it may be concluded that it is a feature consistent with a relatively high order of development in exact accord with the principles governing parallel changes in the pits of the wood tracheids. They are also in harmony with the well-known principle that variation is always of a more simplified form in primitive types, but that it tends to greater diversification with advance in organization and general development, as a necessary sequence to the adjustment of the organism to a wider and more complex environment. Finally it has been shown that the elimination of the bordered pit proceeds concurrently with the more complete organization of the ray tracheids, in response

to a substitution of functional activities between these structures and the degenerate parenchyma cells. We may therefore conclude that extreme variation in the character of the pit is an expression of a higher type of development, and that from this standpoint, such structures have a definite value in solving questions of descent.

The terminal walls of the ray cells present three variants with respect to secondary growth. All the more primitive Cordaitales and Coniferales are characterized by thin walls. Cupressus and Juniperus are chiefly distinguished by their thin walls which are also locally thickened, a feature which has been shown to be due to incipient secondary growth. But such alterations are already foreshadowed in Libocedrus where the local thickening of the wall is of a sporadic nature. In *Abies magnifica* and *A. grandis* there is a partial recurrence of thin and locally thickened walls, which is pretty fully expressed in *A. concolor*. A similar recurrence is met with in *Pseudotsuga macrocarpa*, in *Picea polita* and in *Pinus parrayana*, and it is also complete in thirteen of the most highly developed species of Pinus, where the walls have suffered extreme degeneration. Within the limits of Picea (1) and the soft pines (5), there are six instances in all, of sporadic and partial survival of the thin and locally thickened wall. The first tendency to thick and strongly pitted walls is manifested in five species of Juniperus, and such development is fully expressed in what may be regarded as the three most highly developed species. Thick walls are then fully characteristic of Abies — with a partial reversion in *A. concolor*, of Tsuga, *Pseudotsuga douglasii*, Picea, with the exception of *P. polita*, five species of soft pines and three species of hard pines. In *P. tæda* and *P. palustris* the walls are so degenerate that their structure cannot be satisfactorily determined, but they are presumably thin-walled.

From these facts it is manifest that the progressive thickening of the terminal walls accords with the general course of development, and once more making use of the principles already applied to the pits on the lateral walls, we are brought to the natural conclusion that (1) an increase in the thickness of the walls is evidence of a higher type of organization, and (2) that

the sporadic recurrence of thin walls with local thickenings represents the persistence of a primitive character.

Ray tracheids probably constitute one of the most valuable of the structural elements as an indication of development. This has its foundation (1) in the fact, previously shown, that they arise as secondary structures from the parenchyma elements, with which they exhibit interchangeable relations, in direct response to the requirements of a higher degree of organization, and (2) their general relation to progressive development. The complete absence of ray tracheids from the Cordaitales and Ginkgoales, as also from the Taxaceæ and more primitive Coniferæ, while they are invariable features of the higher Coniferæ in which they attain their most complete development, admits of only one interpretation. The fact that they are exclusive features of the Coniferæ emphasizes their inferior value for determining the derivation of that group, while it points to their superior importance as a factor in the sequence of the various coniferous genera. They occur sporadically in Thuya (1), Cupressus (2), Juniperus (1), and Abies (1). They are prominent features of Tsuga, Pseudotsuga, Larix, Picea and Pinus. Their invariable absence from Sequoia would appear to suggest that this genus is more primitive than Thuya, but there are other reasons which serve to suggest the opposite relation. Apart from this exception it will be seen that in accordance with the relations exhibited in the table of anatomical data, the genera enumerated form a continuous series, commencing with those showing sporadic tracheids, and ending with those in which such structures attain their highest expression. From this we are justified in the conclusion that the rare occurrence of tracheids in Thuya, etc., is to be interpreted as the first evidence of a tendency in development which is only fully realized at a later period, and this appears to be justified by a closer examination of the last five genera in this respect, since it is found that in them the tracheids not only show a progressive numerical development, but their structure likewise becomes more complicated in direct relation to the evolution of higher types of genera and species. We must therefore look upon the tracheids, with their thin, simple walls, as the primitive form, while those with the

strongest reticulations are of the highest type, the two being united by a transitional form characterized by the presence of simple teeth. The evidence at hand does not appear to justify the idea that the various genera have been segregated into small groups representing side lines of development, but it rather favors the thought that each genus is in itself a complete, short line of descent, and that among these a prominent parallelism has arisen in the tendency toward the development of tracheids — a tendency which has been carried to completion in the case of only five of the series, and in such a way that in only a portion of one of these has that completion reached its highest expression.

The occurrence of two kinds of parenchyma ray cells is an exclusive feature of the genus Pinus, and their value for phylogenetic purposes is strictly confined to the relations of the various species of pines. The first appearance of this differentiation is among the soft pines in *P. aristata* and *P. edulis*. It is to be observed, however, that the thick-walled cells are always dominant, the thin-walled cells being interspersed among and coterminous with them. No further evidences of such structural alterations are to be noted until we reach the more highly developed representatives of the hard pines. Among these definite transition forms occur in *P. murrayana*, *P. coulteri*, *P. jeffreyi*, *P. virginiana*, *P. insignis* and *P. cubensis*, while in *P. arizonica*, *P. ponderosa*, *P. sabiniana*, *P. pungens*, etc., the original relations are exactly reversed and the thick-walled cells show a diminishing frequency, until in *P. glabra* and *P. tæda* they are rarely met with. Such facts give effective proof to the belief that structural alterations of this nature are not only evidences of the highest type of development among the pines, but in the Coniferales as a whole.

The invariable absence of the fusiform ray from all except the four genera which attain the highest structural development, and their constant occurrence in all the species of such genera, presents an argument of great force as showing their relation to the evolution of advanced types. There is here no evidence of sporadic development, foreshadowing the general course of evolution, but the fusiform rays with their resin canals appear

abruptly and permanently. Among fossil plants — except the genus Pityoxylon which, being essentially Pinus, falls under the general rule — there is no instance of such structures outside of the four genera named, save in the case of the remarkable *Sequoia burgessii*, from the Lignite Tertiary (4, p. 242) and *S. penhallowii* of Jeffrey. As it will be necessary to further discuss the essential structure of the fusiform ray when considering the resin passages in particular, it will be unnecessary to deal with it more at length at the present moment.

Errata.

Page 249. For Cordaite*d* read Cordaite*s*.
Page 263, Fig. 12. For Radial read *Tangential*.

(*To be continued.*)

FURTHER INSTANCES OF MALAR DIVISION.

ALEŠ HRDLIČKA.

By the courtesy of Dr. Horace Jayne, Director of the Wistar Institute, Philadelphia, I am able to report on two skulls, one Peruvian (Indian) and the other that of a Chinese, in both of which is found what appears to be a bilateral, complete, malar division. The specimens and anomalies are as follows:

(1) Spec. No. 53, Wistar Institute, cranium of a male, adult (past middle age), Peruvian Indian. The occiput shows a moderate, predominantly unilateral, baby-board compression. A smaller Wormian bone is present in the left coronal suture and an unusual bone of the same nature, 10 mm. long and 9 mm. in maximum breadth, in the sagittal suture, 28 mm. posterior to bregma. The skull shows no pathological lesion, no signs of traumatism, and no marked anomalies besides those to be described.

Each of the malars is completely divided by an antero-posterior suture into a smaller lower and larger upper portion. The condition is very much alike on the two sides and offers a number of points of special interest. (Fig. 1.)

The body of each malar is very narrow (antero-posterior diameter, dorsally, at middle, 13.5 mm. on the right and 12.5 mm. on the left). This narrowness is caused by an unusual development and extension backward of the malar process of the superior maxillary. The central part of the malar bone was apparently belated in development and a compensation for the defect by the maxillary took place.

The upper, larger portion of each malar shows in its zygomatic border a well marked, 5 mm. long, slightly dentated suture corresponding to the occasional posterior incomplete suture of the normal malar. This suture is supposed to be the remnant of the embryonal separation between the parts of the malar that develop from respectively the superior and inferior center

of ossification of the bone. If this theory is correct, which thus far there is no reason to doubt, then we have here a clear case of an appearance of a separate, submalar center of ossification. The case would then be not a divided malar, but an imperfectly developed malar, with a *sub-malar.*

FIG. 1.— Right Malar of a Peruvian Indian, showing an Antero-Posterior Complete Division and above that a Posterior Incomplete Suture.

Ventrally the anomalous suture is in every respect very much like dorsally. From each of the incomplete sutures in the zygomatic border of the malar proper runs a shallow groove, such as was described by Gruber, forward, reaching on the left the malo-maxillary suture.

The upper portion of the right malar shows one, that of the left two nutritive foramina.

This is the second instance of a malar suture observed in an American Indian[1] and in both cases the subject was a Peruvian.

Measurements of the Malars.

	Right.	Left.
Height anteriorly (bet. the ends, dorsally, of the malo-maxillary suture)	33.5	32. mm.
" at middle	34.5	?
" posteriorly (dorsally: bet. lowest point of malo-zygomatic and most posterior point of malo-frontal suture)	44.	44. "

[1] The first instance was reported by me in the *Amer. Nat.*, April, 1902 ("New Instances of Complete Division of the Malar Bone, with Notes on Incomplete Division," pp. 273–294).

Measurements of the Malars (continued).

	Right.	Left.
Breadth antero-superiorly (dorsally: bet. the superior extremity of the malo-maxillary and the anterior end of the malo-frontal suture)	33.	34. mm.
" at middle	13.5	12.5 "
" inferiorly (bet. lowest points of the malo-maxillary and malo-zygomatic sutures)	25.	25. "
Vertical height of the inferior malar portion, to the malar suture, anteriorly	13.	?
posteriorly	8.5	? [1]

(2) Spec. No. 7217, Wistar Institute, cranium of a male, adult (below middle age) native of China. Skull dolichocephalic, normal. Upper third molars rudimentary; styloids very rudimentary. A small epipteric on left, on right a large epipteric (41.5 mm. long, 10 mm. high), and several episquamous ossicles more posteriorly.

Fig. 2.—Left Malar of a Chinese, showing a Complete Antero-posterior Division.

Both malars consist of a larger superior and a smaller inferior portion, separated by an antero-posterior moderately dentated suture, 21 mm. long on the right, 19 mm. on the left side. (Fig. 2.)

Ventrally the aspect is entirely different. On the left a tapering process from the maxilla reaches and articulates with the zygoma; on the right a similar process exists, but ends within 3 mm. of the zygoma. Both processes cover the malar suture anteriorly and posteriorly, but in the middle leave it, and

[1] The lower malar portion on the left has been lost.

also an island-like part of the superior portion of the malar, uncovered.

The separate inferior portions of the malars resemble somewhat those in case 1

Measurements of the Malars.

	Right.	Left.
Height anteriorly	36.5 mm.	35.5 mm.
" at middle	36.5 "	35.5 "
" posteriorly	51.5 "	49. "
Breadth antero-superiorly	38.5 "	37.
" at middle	24.5 "	23.5 "
" inferiorly	32. "	32.5 "
Vertical height of the inferior malar portion, to the malar suture,		
anteriorly	11.5 "	11.
posteriorly	9. "	8.

To the above two cases I am able to add the following recent observations of malar suture in the U. S. National Museum:

(a) Skull of a male, middle aged Chickasaw Indian (No. 227, 483, Dep't. of Anthrop., U. S. N. M.). This specimen, recently returned from the Army Med. Mus., was brought to my attention by Dr. D. S. Lamb. Skull shows a somewhat premature closure of sagittal and coronal sutures.

Each malar is divided, in very much the same manner, by an antero-posterior suture into two portions. The lower of these, nearly of an equal extent throughout, is at middle on the right 10 mm., on the left 9 mm. high; the height of the upper portion at middle is on the right 22 mm., on the left 21 mm.

The anomalous suture is on the right as well as on the left dorsally 15 mm., ventrally on the right 5 mm., on the left 6 mm. long. It is shortened by a wedge-like process of the superior maxilla, identical in appearance and only of a slightly lesser extent, to that in the above described, Wistar Institute Peruvian. The upper portion of each malar shows one moderate size foramen, but no incisure.

There are no further anomalies on the cranium.

Among 380 skulls of apes and monkeys[1] in the Department of Biology of the Museum, in which the malar sutures are clearly traceable, there are three, a Macaque, a Cercopithecus, and a Chrysothrix, with malar division.

FIG. 3.— Divided right malar of *Macacus pelops*. Natural size.

(b) Macacus pelops, male, adult, No. 22,062. The right malar shows an oblique, serrated division, running dorsally from a short distance above the lower end of the malo-maxillary suture to the curving superior border of the zygoma (Fig. 3). The ventral part of the suture lies in nearly the same position. On the left is found dorsally a 4 mm. long suture, beginning from the malo-maxillary suture in a similar position as that on the right side. The two malars are equally high and long. The skull shows no other anomalies.

FIG. 4.— Divided zygomatic process of *Ceropithicus callitae*. Natural size

(c) Cercopithecus callitrichus, male, adolescent, No. 16, 365. The right zygomatic process is posteriorly completed by a triangular portion, separated from the main part by a suture. Superiorly the border of the malar portion of the arch just touches that of the temporal portion, inferiorly the two are separated by a distance of 12 mm. (Fig. 4.) The supernumerary suture is serrated and equally well distinct ventrally. It is very plainly anomalous in character; there is not the slightest trace

[1] 1 Chimpanzee, 1 Gorilla, 2 Orangs, 8 Gibbons, 12 Cynocephali, 3 Symphalangi, 1 Nasalis larvatus, 6 Simias concolor, 55 Presbytes, 24 Semnopitheci, 116 Mascagues, 22 Cercopitheci, 10 Colobi, 5 Cercocebi, 15 Mycetes, 6 Alonata, 57 Ateles, 1 Lagothrix, 40 Cebi, 6 Hapale, 4 Midas, 4 Nictipitheci, 1 Saimiri, and 7 Chrysothrix.

of any traumatism. The dimensions of the two malars are almost identical, even inferiorly. The specimen shows no other anomaly.

(d) Chrysothrix (Venezuela), male, adolescent, No. 35,800. On the left side is present an anomalous separation of the zygomatic process from the body of the malar. (Fig. 5.) No trace of any traumatism. On the right the zygomatic arch has been lost. The specimen shows no further anomaly.

Fig. 5.—Divided zygomatic process of Chrysothrix (Vener). Natural size.

No one of the three monkey skulls here mentioned was in any way pathological.

In a number of Presbytes Semnopitheci, one Hylobates, one Symphalangus, five Macaques, and one Ateles, a more or less pronounced marginal cleft or fissure was seen in the superior border (frontal process), three to five mm. externally to the edge of the orbit, running to a foramen.

There were found in the series no clearly defined anterior or posterior partial malar sutures.

The above six cases present a number of new points and will be of value in the eventual summing up of the whole subject of malar divisions.

Several interesting cases of the anomaly in man and mammals, including an orang, have also recently been reported by Frassetto (Notes de Craniologie Comparée, Ann. Sc's. Natur., Paris, Sept. 1903).

U. S. National Museum.

STUDIES ON THE PLANT CELL.—I.

BRADLEY MOORE DAVIS.

Introduction.

This is the first of a series of papers that will follow one another in the pages of the *American Naturalist*. They will describe the chief structures in plant cells and the most important events in their life histories, largely from the point of view of the morphologist and student of developmental processes. Research upon the plant cell has entirely outrun the general accounts that may be found in several botanical text books and in certain works of prominent zoölogists. We shall attempt to give a general survey of the subject in its present state with references to the most important papers; but this is not to be an exhaustive account of a literature that is already very large and which can probably be treated far more satisfactorily several years from now when it has passed through the criticism that time will give in a field of very active botanical investigation.

American botanists have reason to be proud of the achievements of their countrymen in research upon the morphology and physiology of the plant cell, for much of the best work of recent years has come from them. This in itself has been a great stimulus to the writer to prepare these brief accounts which he hopes will assist the general botanist to a clearer understanding of the progress in this field. They will also serve to contrast the protoplasmic activities among plants with those of the animal cell which has been so well treated in several foreign works and in English by Wilson's *The Cell in Development and Inheritance*.

The author will feel especially gratified if these papers should help to change an attitude towards investigations on the plant cell that is unfortunately too prevalent among botanists. There is a tendency to regard cell studies as a very special field of botanical research with elaborate technique which the average

botanist cannot be expected to master. Those who work in this field are considered as in a department by themselves and are labeled cytologists which is sometimes given as an excuse for knowing little about their results. Cell studies are nothing more than morphological and physiological investigations which are frequently so broad as to break the mould of the narrower morphology and physiology of former years. Cell studies must be the foundation of all exhaustive work in morphology and physiology. Indeed among the lower plants they constitute almost all there is to morphology and will determine the classification and relationships of great groups. There are no better illustrations of this fact than the effect of Prof. Harper's investigations on the ascus and sporangium upon Brefeld's theory of the origin of the Ascomycetes. And again the results of several investigators upon the multinucleate gametes found among the Phycomycetes and Ascomycetes are of the utmost importance to a correct understanding of the phylogeny of these groups. When students of the plant cell refuse to accept the stamp of cytologist and insist and show that their work is simply fundamental morphology and physiology we shall break away from a past that should be outgrown.

The material of these papers will be treated under the following heads.

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Literature on the Plant Cell.

Reference to special papers will be given by the authors name and the date of publication through lists presented at the end of every section.

There is no comprehensive treatise devoted to the plant cell but the following general accounts and reviews of the literature are important.

1. Strasburger in the *Lehrbuch der Botanik* and Pfeffer in his *Physiology of Plants* present the best general accounts of the structure and activities of the plant cell.

2. Zimmerman in 1893 and '94 (" Beihefte zum Botanischen Centralblatt " vol. 3 and 4), reviewed the literature on the plant cell under the title " Sammel–Referate aus dem Gesammtgebiete der Zellenlehre " and in 1896 collected the literature dealing with the nuclei of plants in a book entitled *Die Morphologie und Physiologie des pflanzlichen Zellkernes*, Jena, 1896.

3. Dangeard discusses a number of cytological topics in the 6th series of *Le Botaniste* (1898) with especial reference to his studies on the Chlamydomonadineae.

4. Fischer, *Fixirung Farbung und Bau des Protoplasmas* Leipzig 1899, presents a critique of the methods of cytological research and the justification of the conclusions based thereon.

5. The most recent analysis of conspicuous activities of the plant cell is that of Strasburger *Ueber Reductionstheilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich, Histologische Beiträge* VI, 1900.[1]

Section I. Structure of the Plant Cell.

It is customary to apply the term cell in Botany not alone to the protoplasmic units of organization but also to the enclosing wall that generally surrounds the protoplasm. Indeed these walls alone when entirely emptied of protoplasm in specialized

[1] To this list should be added an excellent concise review by Koernicke entitled "Der heutige stand der pflanzlichen zellforschung " *Ber. d. deut. bot. Gesell* 21, (66), 1904. This article appeared too late to be quoted in the earlier papers of this series.

regions of the plant, *e. g.* vascular and certain supporting and tegumentary tissues, are still called cells. When among the lower forms and at certain periods in the life history of many higher plants the protoplasm is naked (*e. g.* zoöspores, sperms, eggs, etc.), these structures are cells in exactly the sense used by zoölogists. We shall consider almost entirely the protoplasmic portion of the plant structure for any extended treatment of the walls would lead us at once into that field of microscopic anatomy termed histology.

1. Protoplasmic Contents.

The most highly differentiated region of the cell is the nucleus, a structure remarkably uniform in organization among all plants except the lowest Algæ and some very simple Fungi. These more primitive conditions will be considered in Section VI. Besides the nucleus there are present plastids in all groups except the Fungi. Plastids are likewise specialized protoplasmic elements although much simpler in structure than the nucleus. Nuclei and plastids lie in a protoplasmic matrix called the cytoplasm. Cytoplasm is more variable in structure and activity than any other region of the cell. Thus three forms of protoplasm, nucleoplasm, plastidplasm and cytoplasm comprise all the living material of the cell and may be sharply contrasted with the non-protoplasmic contents, mostly food material and waste products, which will be considered under a separate head. Definite masses of nucleate protoplasm, with or without plastids are termed protoplasts and such are either unicellular organisms themselves or units of a multicellular structure.

(a) The Nucleus.

The nucleus is bounded by a delicate membrane that is probably largely or wholly a modification of the surrounding cytoplasm. The nucleoplasm very rarely completely fills the nuclear membrane, the remaining space being occupied by a fluid known as the nuclear sap. The elements in the resting nucleus consist chiefly of material that takes the form of a net work so that the

effect is that of a much coiled and twisted thread whose loops are united at intervals to form large and small meshes. The ground substance of this thread is called linin and imbedded in it as in a matrix are deeply staining granules of chromatin. Chromatin is regarded as the most important substance in the nucleus, chiefly because of its behavior during nuclear division, and in critical periods of the life history of organisms as at sporogenesis, gametogenesis and fertilization (to be described in Section V). Just before nuclear division the chromatin becomes organized into bodies named chromosomes which are remarkably uniform in number and definite in shape for each tissue and period of the plant's life. They will be discussed under "The Events of Nuclear Division" (Section II), and in Sections IV and V.

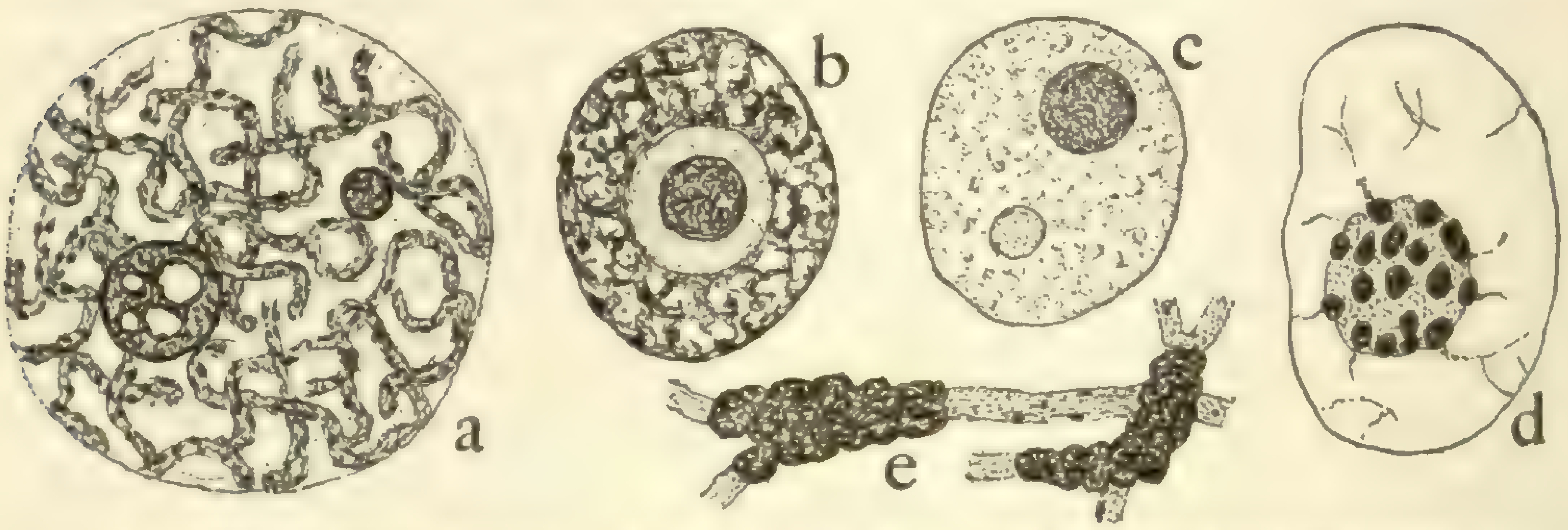

FIG. 1.—The resting nucleus. *a*, Embryo sac of lily with linin thread and two nucleoli. *b*, Root of onion large nucleolus. *c*, Tetraspore of Corallina showing large chromatin body and small nucleolus. *d*, Spirogyra with central body containing chromatin. *e*, Chromatin on linin net work from egg of pine. After Mitzkewitsch and Chamberlain.

In the meshes of the linin network or lying freely in the nuclear sap may be found one or more bodies, generally globular in form, called nucleoli. (See Fig. 1 *a* and Fig. 1 *b*). The nucleolus is generally regarded as a secretion of the nucleus and it is quite certain that its substance is utilized just previous to and during the period of nuclear division when the spindle is formed. (Strasburger '95 and :00, p. 125, and from the work of others). The structure is not always homogeneous but may show in the interior small vesicles or areas of a different consistency from the periphery. There is often present also a rather thick outer shell or membrane. Sometimes the chromatin in the nucleus may be gathered into a globular body that resembles superficially a nucleolus. Such chromatin bodies are gen-

erally transitory as in Corallina, Davis '98, where the structure (Fig. 1 *c*) is only found in the young daughter nucleus and later fragments into many smaller bodies. In Spirogyra however (Moll '94, Mitzkewitsch '98, Van Wisselingh :00, '02) the chromatin is supposed to be always in a globular mass mixed with nucleolar substance and recalls the conditions in certain Protozoa. These chromatic structures however should never be confused with nucleoli, whose substance is different and which are not permanent in the cell, since they may disappear before or during nuclear division and be formed *de novo* in each daughter nucleus.

The substance of the nucleolus is not well understood. It is frequently impossible to distinguish it from chromatin except when favorably situated in the cell and there is much evidence that it is closely related to that substance. In large nuclei of higher plants the chromatin is sometimes gathered into globular bodies without apparent relation to a linin thread and these are readily mistaken for nucleoli and have been called such, but this loose usage of the term should be avoided. And true nucleoli may be so closely associated with the linin net work as to have the appearance of chromatin. Some of these conditions have been especially described by Cavara, '98. Chamberlain, '99, has made a study of the egg nucleus of the Pine where masses of chromatin may take very irregular forms on the linin threads (Fig. 1 *e*) and sometimes resemble small nucleoli. But such conditions should always be sharply distinguished from true nucleoli which are often caught in the meshes of the linin net work and appear to be a part of it when in reality there are no organic attachments. It is certain that nucleoli are of secondary importance in the cell and probably by-products of the general constructive activities of the nucleus. In which case they may be secretions, perhaps closely related to chromatin, or even direct transformations of this substance. It is well known that the nucleus has wonderful constructive powers, when the amount of chromatin and other nuclear substances may be immensely increased, facts that are especially well illustrated at reproductive periods of the plant's life as during sporogenesis and gametogenesis.

Chromatin is the only substance in the nucleus that is constant

in its presence throughout all periods in every cell's history. It passes on from cell to cell through the mechanism of nuclear division without interruption. There are periods of cell history when the nucleus consists only of chromosomes as in the stages of nuclear division called mataphase and anaphase. The other structures of the nucleus have their relation to definite conditions that are in part understood. The nuclear membrane probably results from the reaction of the cytoplasm to the secretion of nuclear sap among the chromosomes (Lawson, :03 *a*). It would then be strictly cytoplasmic in character and similar to the plasma membranes around vacuoles. Nucleoli must be regarded as temporary structures since they generally disappear during nuclear division either dissolving or else passing out into the cytoplasm where they may remain for long periods as deeply staining globules (extra nuclear nucleoli). Linin is believed to be derived from chromatin and in its turn may be transformed into the substance of spindle fibers, which are cytoplasmic, so that chemically it holds a position somewhat intermediate between chromatin and cytoplasm. It seems established that the linin net work is a temporary structure related to the activities of chromatin.

(b) The Plastids.

These very interesting structures, characteristic of plant cells, have not received the degree of attention that they deserve and much valuable work may be done in the detailed study of their protoplasmic structure and activities at various periods of ontogeny especially through the series of changes that are presented during developmental processes.

The primitive types of plastids are relatively large structures, often solitary in the cells, and generally of complex form. These are called chromatophores and are characteristic of many algæ especially among the lower groups but are not found above the thallophytes (Anthoceros and Selaginella excepted).

The chromatophores of the simplest algæ are replaced in most of the higher types of these thallophytes and in all groups above by very much smaller structures, generally discoid in

form, which are called chloroplasts when green, chromoplasts when the color is other than green or leucoplasts if colorless. These plastids are without doubt derived from the more primitive chromatophores.

The colors of chromatophores are various. They are believed always to contain some chlorophyll but this green is frequently so completely masked by other pigments that its presence can only be determined when the additional coloring matters have been extracted. Chloroplasts are universally green except when they may be changing into chromoplasts. Chromoplasts generally take their tint from the predominance of other strong pigments in addition to chlorophyll as phycœrythrin in the red and phycophæin in the brown algæ. But chromoplasts may be derived from chloroplasts whose green has largely or wholly disappeared leaving other pigments present as the yellow, xanthophyll, or the orange red, carotin.

The remaining plastids, leucoplasts, are devoid of color and are found in embryonic regions such as eggs, growing points, and in the various tissues of seeds, underground organs and other structures where the cells are largely or wholly removed from sunlight. The leucoplasts may become green upon exposure to light thus changing into chloroplasts. They are responsible for the secretion of reserve starch in many structures (*e. g.* potato) and in consequence have been called amyloplasts.

Leucoplasts, chloroplasts and chromoplasts are morphologically the same structures. It is well known that they may pass one into the other in the order indicated and that chloroplasts and chromoplasts may lose their color and become leucoplasts. It is generally believed that plastids are not formed *de novo*. They divide by constriction and thus multiplying are passed on from cell to cell and it is believed from generation to generation. They are therefore usually ranked as permanent organs of the cell. However, it is but fair to call attention to the fact that there are some serious difficulties in the way of a complete acceptation of these views.

The protoplasmic structure of the plastids of higher plants is rather simple while that of the chromatophores in algæ is more complex since they contain a special organ termed the

pyrenoid. The detailed structure of chromatophores was first described by Schmitz ('82) and of plastids by Meyer ('83). The most complete study of plastids however is that of Schimper ('85). The body of the plastid is always denser than the surrounding cytoplasm. It has a porous structure that is only visible under high magnification and there are sometimes present very delicate fibrils. The coloring matter, oily in consistency, is held in the pores as minute globules. The plastid may therefore be compared to a very fine-textured sponge saturated with pigment. All of the coloring matter of the plastid may be readily extracted with alcohol leaving the colorless proteid matrix.

The pigments of plastids are then in the nature of secretions held in these specialized regions of protoplasm. Chlorophyll is the principal substance and, as has before been said, is almost always present, but the amount is sometimes so small that its green is completely hidden by the color of other pigments. Chlorophyll itself contains greater or less amounts of two other coloring matters that may be readily separated from the pure green, a yellow xanthophyll and an orange red carotin, both substances closely related to chlorophyll. The other pigments, characteristic of the chromatophores in some groups of algæ, are however quite distinct from chlorophyll. There is phycocyan, found in the blue green algæ (Cyanophyceæ), phycophæin and phycoxanthin, characteristic of the brown (Phæophyceæ) and phycœrythrin of the red (Rhodophyceæ).

Chloroplasts are found almost universally in green plants above the Thallophytes and are also present in the large group of algæ the Siphonales and in the Charales. They are sometimes formed very numerously in the cell, reproducing rapidly by fission (see Fig. *2 a* 2, 3) and lie in the layer of protoplasm just inside of the plasma membrane. They are sensitive to light and readily shift their position in the cell. Strong illumination results in their retreat from exposed positions to the sidewalls and bottom of the cell where the light is less intense. If the illumination be weak they may all gather on the side most favorable for the reception of light. These facts are well illustrated by the behavior of the plastids in some of the Siphonales (*e. g.*

Botrydium), in the Rhodophyceæ (*e. g.* Polysiphonia) and also in the palisade cells of leaves. Chloroplasts after exposure to light generally contain starch but in some plants this substance is never formed (*e. g.* Vaucheria, Fig. 2 A 1), the first visible products of photosynthesis being other substances more of the nature of oil. It is not known whether the starch grain in the

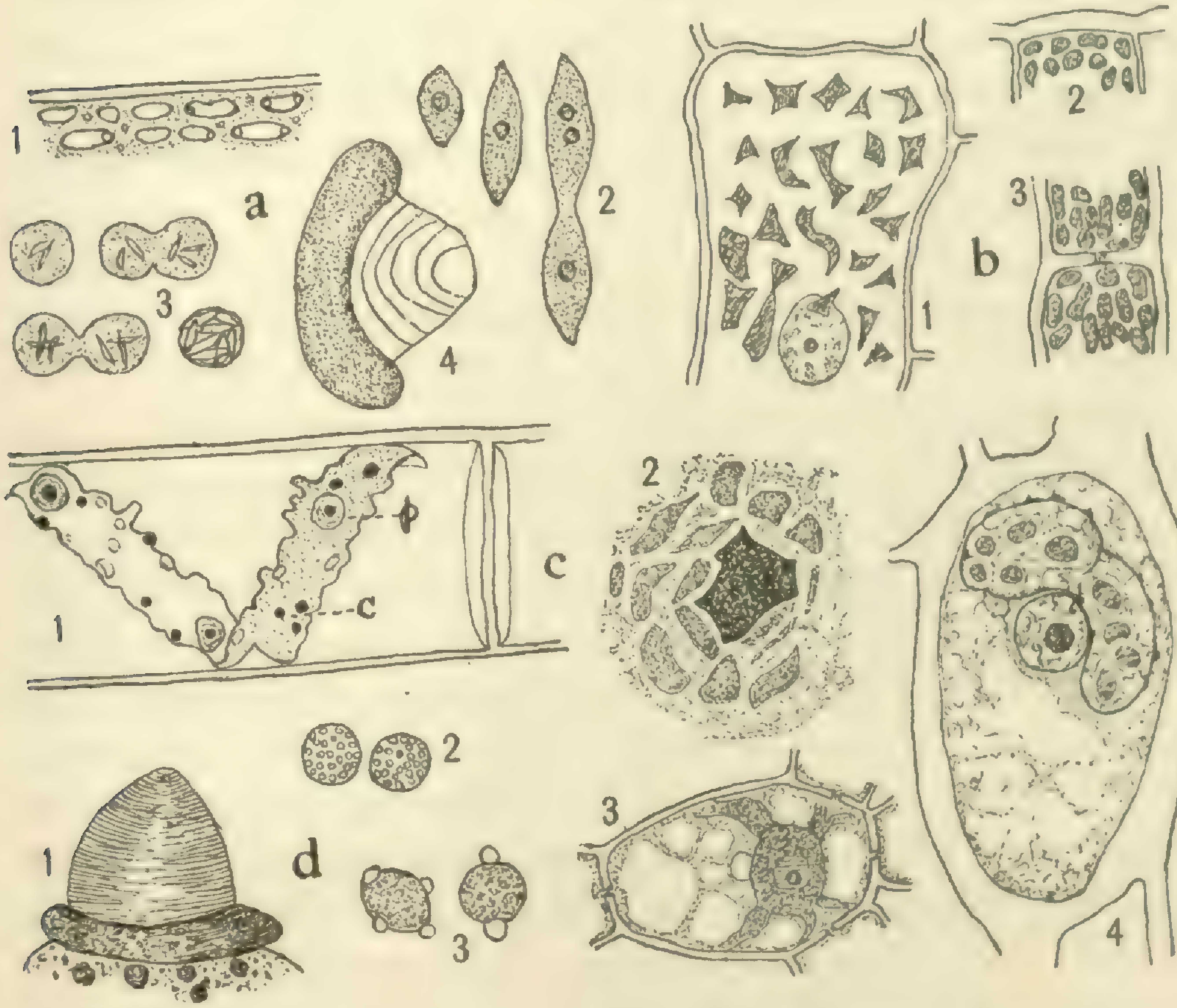

FIG. 2.— Plastids. *a*, Chloroplasts: 1 Vaucheria, with oil globules; 2 Bryopsis; 3 moss (Funaria), in division and containing starch grains: 4 Oxalis, with a grain of starch. *b*, Chromoplasts: 1 Tropaeolum, epidermal cell from calyx; 2 Fucus, 3 Callithamnion. *c*, Chromatophores: 1 Spirogyra, with pyrenoids (*p*) and caryoids (*c*); 2 Hydrodictyon, pyrenoid forming starch; 3 Nemalion; 4 Anthoceros, in division and containing starch. *d*, Leucoplasts: 1 Phajus, plastid and starch grain at the side of the nucleus; 2 Iris, from root and containing oil globules; 3 Iris, in deeper cells of root, with starch grains. After Meyer, Strasburger, Palla, Timberlake and Schimper.

chloroplast results from the direct change of some of the proteid substance or whether it is a secretion. The conditions are somewhat different when pyrenoids are present in a chromatophore as will be described presently.

The chloroplasts of higher plants may change color under various conditions and become chromoplasts. Some of the best

examples are found in the colored cells of certain floral parts and fruits (Fig. 2, *b* 1). These pigments are generally either xanthophyll (yellowish) or carotin (orange red). Chloroplasts may also turn brown especially in older cells that are losing their contents. The colors of some leaves and flower parts are due not to the plastids but to substances dissolved or otherwise held in the cell sap of the vacuoles. The brilliant coloration of autumn foliage is of this character as well as some of the tints of petals, hairs and other structures. The chromatophores of the higher brown Algæ (Phæophyceæ) and most of the red (Rhodophyceæ) have the discoid form characteristic of chloroplasts (Fig. 2 *b* 2, 3). They might be called phæoplasts and rhodoplasts if one wished to classify plastids according to their color.

The structure of chromatophores is frequently complicated by the presence of pyrenoids which may be quite numerous in the body. These structures are denser regions of the chromatophore with a definite boundary. They are proteid in character and are known to vary in size with nutritive conditions and may completely disappear if the cell is starved. They have been regarded as masses of reserve proteid material but certain functions of great importance are also associated with them. The arrangement of starch grains in the chromatophores of many algæ is clearly around the pyrenoids as centers. For this reason they have been called amylum centers. Timberlake (:01) has recently shown in Hydrodictyon that segments are split off from the pyrenoids (see Fig. 2, *c* 2) and changed directly into starch grains which naturally lie for a time close to the source of their formation and only later become distributed throughout the chromatophore. It is probable that similar conditions will be found in other algæ (Conjugales, Protococcales, etc.) and we may soon have a much clearer understanding of the pyrenoid. The indications are that the pyrenoid will prove to be a region of the chromatophore differentiated as a metabolic center, more or less prominent according to conditions of nutrition, and that its most conspicuous activity is the formation of starch by the direct transformation of portions of its substance.

Some other structures besides the pyrenoids have been

described by Palla ('94) in the chromatophores of several of the Conjugales and have been named caryoids. Caryoids (Fig. 2, *c* 1) are smaller and more numerous than pyrenoids and are distributed irregularly in the chromatophore but chiefly along the edge. Their function is not known.

The leucoplasts complete the list of plastid structures. They are colorless and may be found in underground or other portions of the plant removed from light or where there is little or no photosynthetic activities as in embryo sacs, seeds, growing points, etc. They become impregnated with chlorophyll under conditions suitable for photosynthesis thus changing into chloroplasts. An important function of the leucoplast is the formation of reserve starch in various parts of the plant. The more recent investigations of this process (Meyer, '95, Salter, '98) claim that it is in the nature of a secretion within the substance of the leucoplast. This view is opposed to the older conceptions (Schimper, '81, Eberdt, '91), which regarded the starch grain as formed by the direct change of proteid material in the plastid. In view of Timberlake's (: 01) studies on the pyrenoid of Hydrodictyon we may well hesitate to fully accept the views of Meyer and Salter and ask for further investigations of this very difficult subject. In addition to starch leucoplasts may contain proteid crystals and oil globules.

The reproduction of plastids and their evolutionary history in ontogeny and phylogeny offers a very attractive field for research. It is well known that plastids multiply by fission and it is generally believed that they never arise *de novo* but are passed from generation to generation as permanent organs of the cell. The process of division may be very favorably studied in the spore mother-cell of Anthoceros (Fig. 2, *c* 4). The fission begins (Davis, '99) by a constriction at the surface as though the bounding membrane of cytoplasm exerted pressure upon an elongating structure. There is no evidence that the interior of the chloroplast undergoes any changes that could assist the process further than a possible tendency of the two separating portions to gather their substance together as division proceeds. The conditions suggest that the division is a mechanical separation of material too bulky for the best advantages of the cell,

for the proper balance of protoplasmic elements in narrow confines, a division prompted by the activities of the cytoplasm rather than emanating from within the plastid.

The view of the permanence of the plastid as a cell organ has received its strongest support from the classical work of Schimper ('85). We are not prepared to deny it and to assert that the plastid may arise *de novo.* Yet those who study the cells of embryonic tissues and reproductive phases know that it is extremely difficult to follow the plastids and that these structures require other than the usual methods of cell research to establish their presence. Several writers (Eberdt, Dangeard, Husek and others) have expressed their belief that plastids may arise *de novo* but no one has thoroughly traced the appearance or disappearance of these structures in any cells.

The plastid in phylogeny has never received the attention that it deserves. Beginning with the conditions among the Cyanophyceæ and the lowest Chlorophyceæ (which will be further discussed in Section VI) we find the pigment distributed so generally throughout the cell that it is doubtful if the term chromatophore should ever be applied to regions so indefinite in outline. Above these groups the pigment is confined to proportionally smaller areas in the cytoplasm and these become chromatophores when their form is clear. The primitive chromatophores were solitary and filled a large part of the cell. The pyrenoids arose in the chromatophores probably as the result of the influence of metabolic centers upon the protoplasm. It is scarcely possible that a large chromatophore should be absolutely homogeneous throughout; there would develop one or more centers of metabolic activity and such would exert some influence on the form of the protoplasm.

But the large single chromatophore does not seem to be the form best adapted to the work of a cell perhaps, if for no other reason, because it requires a mechanical adjustment of other cell organs to itself and would interfere with the quick circulation of material and the general balance of cell activities. It seems possible that mechanical difficulties may have led to the division of large chromatophores and the substitution of numerous small plastids. This change was instituted in the

higher members of the Phæophyceæ and Rhodophyceæ and in the Siphonales, Charales, Cladophoraceæ and some smaller groups of the Chlorophyceæ. The Conjugales whose chromatophores are especially elaborate have cells essentially solitary in their life habits and with a very remarkable adjustment of the cell organs to one another to give almost perfect symmetry. With the splitting up of the chromatophore came the loss of the pyrenoid and the final result was the compact plastid so characteristic of plants above the thallophytes.

(c) Cytoplasm.

There is no region of the plant cell that maintains such varied relations to its environment and performs so many visible activities as the cytoplasm. For this reason the accounts of its structure and behavior have been diverse and there has developed a nomenclature of its parts that is confusing and somewhat difficult to harmonize.

Strasburger has for many years (since 1892) employed the term kinoplasm to distinguish an active portion of the cytoplasm (concerned with the formation of spindle fibers and other fibrillæ, centrospheres, centrosomes, cilia, plasma membranes, etc.) from more passive nutritive regions which he called trophoplasm. Kinoplasm corresponds closely to the archoplasm of the animal cell (Boveri, 1888). This classification has been criticised especially by Pfeffer (:00) on the ground that it employed names signifying physiological differences when the distinctions as far as we know are those of morphology alone. However the physiological behavior of kinoplasm and trophoplasm becomes very real to anyone who studies extensively cell activities and the morphological characters serve to emphasize these peculiarities. The truth seems to be that cell studies cannot be pursued from the standpoint of physiology or morphology alone but must combine these attitudes. And in the union it is hardly possible or perhaps desirable to construct a terminology with strict regard to either field of study. We shall use the terms kinoplasm and trophoplasm grouping the various cytoplasmic structures under these heads.

Cytoplasm has surface contact with three conditions and in each case there is present a delicate plasma membrane, colorless and very finely granular, which is very different in structure from the cytoplasm within. The first of these three membranes is the outer plasma membrane, which bounding the protoplast, is consequently just inside the cell wall. This membrane is called the "hautschicht" by the German botanists, a word for which we have no exact equivalent, the term ectoplast more nearly expressing the meaning than any other but for several reasons not being very satisfactory. Since this outer plasma membrane lies against a moist cell wall it is virtually surrounded by a film of water. The functions of the cell wall in land plants and its developmental history indicate a close relation to the demands of the outer plasma membrane for a fairly uniform environment of moisture, a matter which will be discussed in the last section of these papers.

The second form of plasma membrane surrounds the water vacuoles in the cell. It is very common for the plant cell to have a single large central vacuole containing the cell sap and the membrane around this was named the tonoplast by DeVries in 1885. DeVries believed that this vacuole reproduced itself by fission with each cell division and consequently was a permanent organ of the cell. It is, however, now well known that the large central space containing cell sap is not different from other vacuoles, indeed is frequently formed by the flowing together of several small vacuoles as smaller soap bubbles unite in the froth to form a larger one A vacuolar plasma membrane is of course bathed by water since it holds the cell sap and its relation to a moist surface is therefore more evident than in the case of the outer plasma membrane.

The third plasma membrane encloses the nuclear sap with the protoplasmic nuclear elements chromatin, linin and the nucleolus. This nuclear membrane was discussed in connection with the nucleus of which it is generally considered a part, but as there stated, the evidence largely indicates that it is cytoplasmic in character, representing a reaction of this protoplasm to the fluid nuclear sap formed around the chromosomes in the daughter nuclei after each division (Lawson :03[a]). The nuclear sap

necessitates the development of a vacuole which becomes bounded by the nuclear membrane. The nuclear membrane in some cases at least differs from a vacuolar membrane in being easily distinguished from the surrounding cytoplasm as a definite film.

The structure of all the plasma membranes is much the same as far as the microscope may determine. The protoplasm is dense, colorless and filled with very minute granules (microsomata). There are no large inclusions such as plastids, particles of food material (starch, proteids, oils, fats, etc.), mineral matter or waste products. These are all held well within the cytoplasm between the outer plasma membrane and the vacuoles. There is good reason to believe that the substance of all plasma membranes is much the same since they perform very similar activities both in relation to the fluids that bathe them and also because their substance in certain cases becomes the protoplasmic basis of cellulose walls. These resemblances are well established for the outer plasma membrane and that which surrounds the vacuoles. Thus, the capillitium of Myxomycetes (Strasburger, '84) is formed from the plasma membranes around the vacuoles after the same method as a cell wall from the outer plasma membrane. And again, during cleavage by constriction (see section II) in the plasmodium and sporangium of the molds (Harper, '99 and :00, D. Swingle, :03), vacuoles fuse with cleavage furrows from the outer plasma membrane to form a common membrane which surrounds each spore mass and secretes a wall, thus showing identity of function and structure. The resemblances are less conspicuous for the kinoplasm of the nuclear membrane, only appearing indirectly with certain events of cell division (the formation of the cell plate) which will be discussed in the next section of the paper. The evidence indicates that the three plasma membranes are all kinoplasmic in character, a generalization of some importance since it offers explanations of many peculiar cell activities to be described later.

Since all plasma membranes have these common characters it may well be questioned whether an elaborate terminology is justified for structures so closely related. The terms ectoplast and tonoplast seem undesirable since they were meant to indi-

cate peculiarities of structure and a degree of permanence as cell organs that is not actually present. It seems hardly necessary to define the plasma membranes further than by their position in the cell as the outer, vacuolar and nuclear membranes.

All of the cytoplasm bounded by the plasma membranes with the exception of certain conditions to be described later (centrospheres, centrosomes, asters, filarplasm and blepharoplasts) may be called trophoplasm since it contains structures and substances especially concerned with nutritive functions. Trophoplasm presents an open organization in sharp contrast to the dense kinoplasm. This peculiarity is due in part to numerous small vacuoles which give a spongy appearance to the usual foam like structure and is further complicated by the inclusion of material not strictly a part of the protoplasm in the form of various sized granules. There are sometimes present fibrillæ that impart a somewhat fibrous texture. We cannot discuss here the theories of the structure of protoplasm, which has not been so extensively studied in plants as among animals, further than to point out that it varies considerably in different regions of the cell in relation to peculiarities that will be described later. There is sometimes presented very typically the foam structure of Bütschli but the introduction of small vacuoles generally gives a spongiose appearance. This subject is critically reviewed by Fischer, '99, and has also been treated in several papers of Strasburger especially in '97.

Three well differentiated organs of the cell, probably trophoplasmic in character, require special mention, *viz.*, cœnocentra, nematoplasts and physodes. Cœnocentra are very interesting protoplasmic centers found in the oogonia of certain cœnocytic fungi among the Saprolegniales and Peronosporales during oogenesis. They appear just previous to the differentiation of the eggs as small bodies sometimes with delicate radiations (see Fig. 3, *a* and 8, *f*), and are found one in each egg origin. They are apt to increase in size as the eggs mature and evidently become the centers of the metabolic activities of the cells, drawing the sexual nuclei into their neighborhood where the latter increase in size (Fig. 3, *a* 2). The cœnocentrum disappears in the ripe oöspore and is consequently an evanescent

structure. It is probably the morphological expression of a dynamic center in the egg. Cœnocentra have been known for several years and have been given especial attention in the recent investigations of Stevens, '99 and '01, and the author (Davis, :03). They will be further considered in our account of Cœnogametes (Section III).

Nematoplasts are exceedingly small rod or thread like

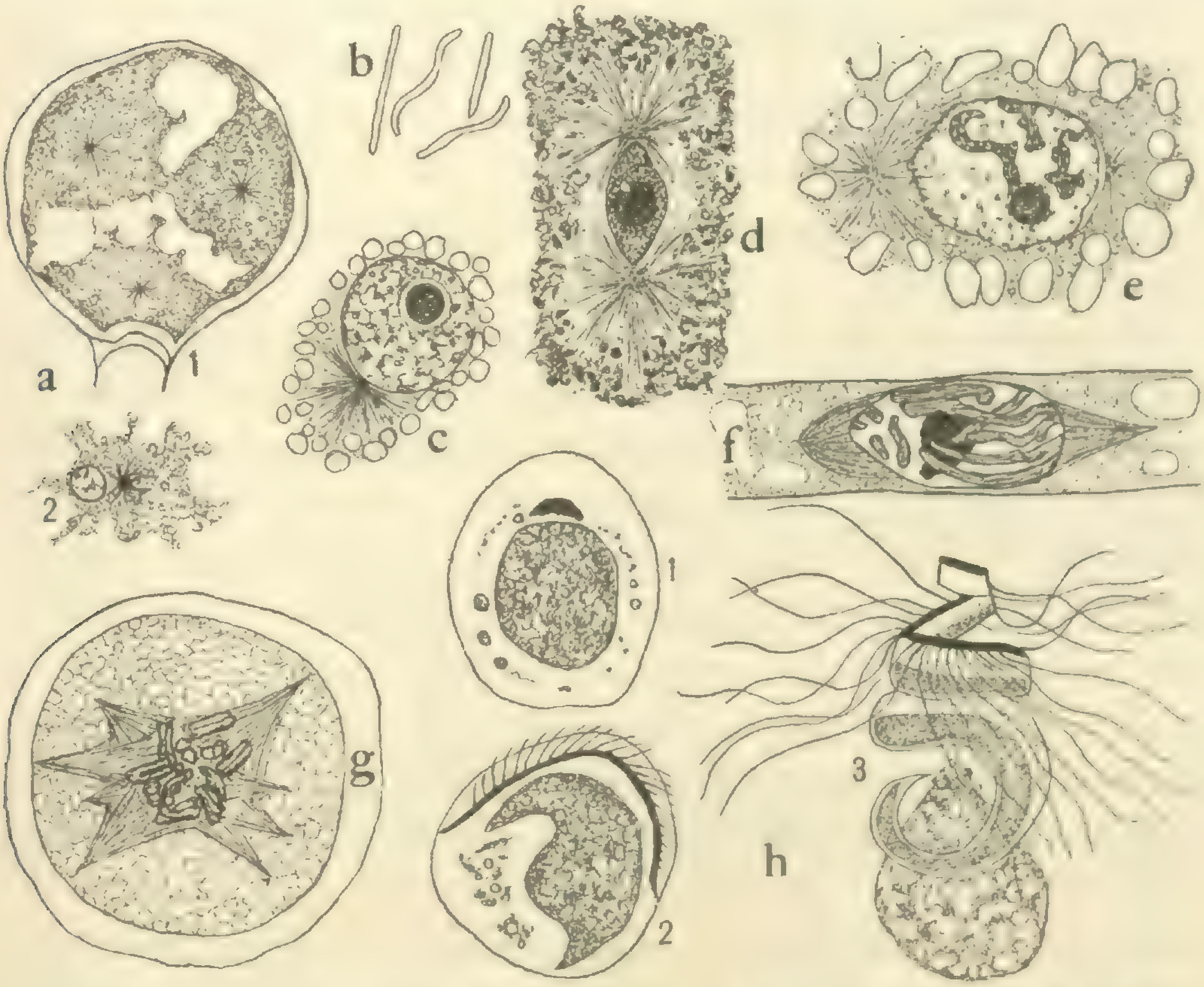

FIG. 3.—Cytoplasmic structures. *a*, Coenocentra of Saprolegnia; 1, oögonium, each egg origin with a coenocentrum; 2, coenocentrum and nucleus from mature egg. *b*, Nematoplasts from hair of Momordica. *c*, Nucleus from apical cell of Sphacelaria, aster with centrosome. *d*, Nucleus from oögonium of Fucus, aster with centrosphere. *e*, Nucleus from germinating spore of Pellia, centrospheres with short cytoplasmic radiations (aster like). *f*, Nucleus from procambium cell of Vicia, kinoplasmic caps. *g*, Pollen mother-cell of Lilium, filarplasm in form of multipolar spindle. *h*, Development of sperm of Gymnogramme: 1, blepharoplast at side of sperm nucleus; 2, blepharoplast elongating and developing cilia; 3, mature sperm, blepharoplast and nucleus in parallel bands, cytoplasmic vescicle below. After Zimmermann, Hof, and Belajeff.

structures reported by Zimmermann ('93, p. 215) in the cells of hairs of Momordica and the root of Vicia (see Fig. 3B). It is probable that organs described by Swingle, '98, and Lagerheim, '99, under the names of vibrioides are the same as or closely

related to physodes. Swingle found them in some of the Saprolegniales and certain Rhodophyceæ and Lagerheim in Ascoidea. They are probably not uncommon. Nematoplasts may be proteid crystals but there is evidence that they move, bending slowly back and forth, which suggests a higher degree of organization. They should be further studied.

Physodes are bladder like structures described by Crato, '92, in certain brown Algæ. They contain a highly refractive substance which gives them a very different appearance from vacuoles whose structure they resemble in many respects. Very little is known about the contents of physodes and it may well be questioned whether they are really organs of the cell and not vacuoles set apart to hold some fluids or substances other than cell sap.

There are left for us a group of kinoplasmic structures that are especially prominent and sometimes only present during the events of nuclear division and at the times when cilia are formed. They will be discussed in later sections of these papers (Sections II, III, V and VI) and at this time we shall give but a brief statement of their appearances. They are centrospheres, centrosomes, asters, filarplasm and blepharoplasts.

Centrospheres are rather large areas of kinoplasm that sometimes lie at the poles of nuclear figures and to which are attached the fibrillæ that form the spindle and also those that may radiate into the surrounding cytoplasm. If the centrosphere contains a distinct central body, or if such a small structure be present alone at the poles of the spindle it is called a centrosome. Should either structure be accompanied by definite fibrillar radiations the whole is termed an aster. These latter conditions are sometimes very complex and are the most interesting types of structures. Asters with centrosomes are known for the brown algæ in the growing points of Sphacelaria (Fig. 3c), Stypocaulon (Swingle, '97) and the spore mother cell of Dictyota (Mottier, :00). They are also beautifully shown in certain diatoms (Lauterborn, principal paper '96, Karsten, :00). Asters with centrospheres and occasionally but not constantly containing centrosome-like bodies are found in the oogonium and germinating eggs of Fucus, see Fig. 3, *d* (Strasburger, '97[a],

Farmer and Williams, '98). Especially well differentiated asters with centrospheres are present during the mitoses in the ascus, functioning at the end in the peculiar process of free cell formation (Harper, '97). Large centrospheres accompanied by radiations are present during the germination of the spores in certain Hepaticæ (Farmer and Reeves, '94, Davis, :01, Chamberlain, :03), but are less conspicuously shown in some and are entirely absent in other phases of the life history. Remarkably large centrospheres with inconspicuous radiations are known in the tetraspore mother cell of Corallina (Davis, '98). Centrospheres occur in the basidium (Wager, '94, Maire, :02). Centrosomes have been reported during the mitoses in the sporangium of Hydrodictyon (Timberlake, :02). Centrosomes have also been described in other types of the thallophytes but we are justified in asking for further work on these bodies since they are generally without raditions and may not have at all the significance indicated. Neither asters, centrospheres or centrosomes seem to be normally present in groups above the bryophytes, nuclear division taking place in these plants by methods, not found in other organisms, which will be described in succeeding sections.

Vegetative and embryonic tissues of plants above the thallophytes present very different conditions from those described in the foregoing paragraph. The centrosphere is replaced by a less definite structure in the form of a kinoplasmic cap which appears at the ends of the dividing nucleus and determines the poles of the spindle (see Fig. 3, *f*). They have been described in the cells of vegetative points of several pteridophytes and spermatophytes by Rosen, '93, Hof, '98, and Nemec, '99 and :01, and in the seta and late divisions in the germinating spore of the liverwort Pellia (Davis, :01).

The most highly developed conditions of spindle formation are found in the spore mother cells of the bryophytes, pteridophytes and spermatophytes. Here the nucleus becomes surrounded by a weft of fibrillæ which form a kinoplasmic envelope probably derived in part from the nuclear membrane. The fibrillæ are at first quite independent of one another or of common centers. Most of the fibrillæ enter into the spindle

which may in the beginning have several poles (see Fig. 3, *g*), but these generally swing at last into a common axis so that the spindle finally becomes essentially bipolar. The term filarplasm is applied to this free fibrillar condition of kinoplasm without organized centers. Filarplasm is peculiar to plant cells and its remarkable activities in connection with multipolar spindles have only been found in groups above the thallophytes. Centrospheres, centrosomes and asters among the lower plants resemble in general the same structures in the animal cell. But filarplasm presents a higher form of kinoplasmic structure with perhaps the most complex activities known in the process of spindle formation. We shall consider them especially in Section III when treating the spore mother cell.

The blepharoplasts are in some respects the most complex structures derived from kinoplasm. They are most conspicuous in the sperm cells of higher plants (spermatophytes and pteridophytes) but they are undoubtedly present in lower forms and probably in zoospores. The blepharoplast develops cilia as delicate fibrillæ from its surface. The origin and homologies of the blepharoplast are uncertain. In some forms they resemble centrosomes at the poles of the last nuclear figures in sperm tissue. But in other cases they are entirely independent of such spindles, a character which cannot be brought into harmony with the activities of centrosomes. They finally lie one at the side of each sperm nucleus, see Fig. 3, *h*, and with the development of the sperm they follow the spiral twist, when present, as a parallel band (Fig. 3, *h*, 2 and 3). This structure will receive detailed treatment in our account of the sperm (Section III).

2. Non Protoplasmic Contents.

It is not possible to distinguish with certainty all the non-living material of a cell from its protoplasm. We have at one extreme cells from which the protoplasm has almost or wholly disappeared and which are either entirely empty or set apart solely as receptacles for various substances, sometimes waste products and sometimes food materials. In contrast with this

condition are the cells filled with cytoplasm so homogeneous in structure that only the most delicate granules (microsomata) can be distinguished in the clear substance.

Waste products such as mineral matter, resins, certain oils, solutions of tannin and various poisons, such as the alkaloides, may be easily recognized. Most food substances such as starch, proteid grains (aleurone), albumin crystals, oils, fats, etc., are readily separated from the protoplasm in which they lie. But the difficulties are much greater with the smaller particles of proteid material, which are frequently such minute granules as to approach the microsomata in size. These may give to the protoplasm a granular consistency that breaks up the foam or spongiose structure characteristic of the pure condition. These granules are undoubtedly in most cases substances intimately concerned with the metabolism of the cell and are members of the chains of constructive and destructive processes that characterize life phenomena.

The other non protoplasmic structures of cells are vacuoles which are essentially bubbles of fluid lying in the denser protoplasmic medium and surrounded by plasma membranes. The watery fluid of vacuoles contains various substances in solution, carbohydrates such as the sugars glucoses and inulin, mineral salts, asparagin, tannin, alkaloids, etc., and occasionally oil and not infrequently crystals. Vacuoles may be formed in large numbers in protoplasm. They tend to run together as do bubbles in a froth and in this way the large central vacuole becomes established in the cell, gathering to itself many smaller vacuoles until the protoplasm is forced to lie as a relatively thin layer next the cell wall. The fluid in the central vacuole (cell sap) is generally thinner and more watery than that in the smaller vacuoles. The latter are apt to be more rich in albumen which may be transformed into proteid grains as is especially well illustrated in the secretion of aleurone. Cell sap may be colored by pigments in solution and the tints of flowers are largely due to this cause alone or to the effects of its color in combination with various plastids in the cell.

It is possible that physodes, described among the cytoplasmic structures, are in reality vacuoles filled with substances other than cell sap, which are not as yet understood.

3. The Cell Wall.

Many of the chief peculiarities of plant organization and activities are due to the presence of the cell wall, its influence on structure and mode of life. The cell wall is not an excretion from the cell like a mineral shell but is formed by the direct change of portions of the protoplasm. The regions concerned may be the outer plasma membrane, the vacuolar plasma membrane or the substance that makes up the spindle fibers which form the cell plate. These structures are all kinoplasmic in character and have to do with the formation of cell walls in various ways which will be described in Section II under the topic "The Segmentation of the protoplasm." The transformation of finely granular films of kinoplasm into cellulose is not well understood but there is an evident solution of the granules (microsomata) and the change of the resultant substance into the cell wall. As a chemical process this change means the replacement of molecules of an albuminous nature by those of a carbohydrate substance. The most complete account of the cell wall is that of Strasburger, '98.

Cell walls are chiefly composed of cellulose, but other substances are always present, modifying the structure in various ways to give widely different properties. These modifications are generally due to infiltrations of foreign substances but sometimes cell walls become incrusted with mineral deposits. The group of cellulose compounds is very large and it is extremely difficult to identify the various substances in structures so small as the cell walls. For a detailed treatment of the chemistry of the cellulose group the reader is referred to Cross and Bevans, '95, and for a general account to Pfeffer, :00, p. 480–485. There are microchemical tests for cellulose that give good reactions for most tissues but which cannot be relied upon for some walls (as in fungi and many algæ) yet it is well understood that the cell walls of these organisms are from the biological point of view essentially the same as for other plants. The cell walls of some fungi are very largely composed of chitin.

Several substances known to be present in cell walls give them marked characteristics. Their association with the cellu-

lose is so intimate as to resist very severe treatment and therefore these cell walls are essentially cellulose groups modified chiefly in their physical properties by the presence of foreign substances. The most conspicuous modifications of this character are lignification, suberization and cutinization Lignified walls are permeable to water and gases. Several substances have been separated from the cellulose of lignified walls, among them lignone, coniferin, vanillin, etc. Suberized and cutinized walls are largely but probably never wholly impervious to water and gases; the one is infiltrated with suberin and the other with cutin, substances that resemble one other very closely. Even walls that appear to be pure cellulose have other substance united with them, the most important being pectose and callose. Cell walls frequently become gelatinous or mucilaginous, when the outer layers swell and lose their form or they may be transformed into gums. These changes are well illustrated in the coats of seeds and fruits and among the algæ and fungi. The cells of algæ frequently secrete gelatinous envelopes or sheaths of substances so closely related to cellulose that were they condensed they would form a firm cell wall.

The cell wall may grow in two directions by methods quite different from one another. There is first surface growth which results in a stretching of the cellulose membrane (growth by intussusception). And second there may be growth in thickness by the formation of successive layers of cellulose inside of one another, giving the wall a striated structure (growth by apposition). The second type of growth is chiefly interesting since it makes possible many peculiarities of structure, because the newly formed layers may not be deposited uniformly inside the primary wall. In some cells the secondary thickenings have the form of rings or spirals or a reticulate structure. The reticulate condition passes insensibly into the pitted cell in which the secondary layers cover the greater part of the surface leaving the primary wall only exposed at the pits. Further discussion of these cells falls more within the range of histology than the purposes of this paper.

The cell wall offers a very interesting field of research among the thallophytes and especially in the lower groups where we

may expect to find these envelopes in a fairly primitive condition and may be able to establish the steps in the origin and differentiation of this very important accessory structure to the plant cell.

(*To be continued.*)

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NOTES AND LITERATURE.

GENERAL BIOLOGY.

Plankton of the Illinois River.[1] — Probably the most extensive study of the plankton of any inland waters is contained in Kofoid's report on the organisms of the Illinois river for the years 1894 to 1899. The period of minimum productivity of plankton is January and February; this is followed by rising productivity which reaches its maximum in April, after which there is a gradual decline to winter conditions. Area and depth showed little relation to plankton production. Young waters from springs and creeks contain little plankton, but these waters when impounded in backwater reservoirs develop an abundant plankton. Fluctuations in hydrographic conditions, temperature, and light affect plankton production. Submerged vegetations tends to diminish the production of plankton. The plankton of the Illinois River is largely autonomous and may be estimated at 67,750 cubic metres. The annual variations in this and in the river fisheries show some correlation.

Where did Life begin?[2] — A second edition of Scribner's little book, which attempts to locate the region where life first appeared on the globe, has just been issued. The argument, now familiar to most readers, turns on the gradual cooling of the earth's crust. Naturally the first parts cooled would be the polar regions and here life may have first originated. No good reason is given for selecting the northern rather than the southern regions as the real centre nor is the question of land and water in these regions sufficiently considered. Since primitive organisms were without doubt water-inhabiting, the possibility of a land-covered surface in the region where they were supposed to originate is not without significance. Inconclusive as the argument really is, the whole treatment of the subject is suggestive and stimulating.

[1] Kofoid, C. A. The Plankton of the Illinois River, 1894–1899. Pt. I. Quantitative Investigation and General Results. *Bull. Ill. State Lab. Nat. Hist.*, Vol. 7, Art. 2, pp. 95–629, 50 pls.

[2] Scribner, C. H. *Where did Life Begin?* New York, Scribner's, 1903, 12mo. 75 pp.

Bermuda. — The account of the Bermuda Islands by Professor A. E. Verrill[1] already issued in the *Transactions of the Connecticut Academy of Science* has been published by the author as a separate volume. After a general description of the islands, their physiography and meteorology are considered and this is followed by a lengthy description of the changes in fauna and flora due to man. The geology and marine zoölogy will appear in another volume. The body of information thus brought together will be invaluable to the future student of these interesting islands.

Morgan on Evolution and Adaptation.[2] — A new book on evolution might at first thought seem superfluous, in view of the already enormous literature on this subject, but advancement in knowledge calls for the presentation of fundamental principles in new lights, and no one who examines this book will find it wanting in food for thought. The general reader will find in it a convenient summary of the older views and discussions about evolution, with extensive quotations from the classical writings of Darwin, Weismann, and others. The new point of view, which especially interests the student and justifies the volume in his eyes, is that taken by Bateson (1893) in his *Materials for the Study of Variation*, and by deVries (1901–3) in his *Mutationstheorie*. From this standpoint evolution is not a continuous but a discontinuous process, in which advance is made by distinct steps. New species do not arise by the slow cumulation of fluctuating individual variations in a particular direction, but are born full fledged. A new species thus produced, which deVries calls a mutation, differs from the parental species at first, perhaps, in only a single respect. It possesses some new character not seen in the parents, or it lacks altogether some character possessed by the parents. It breeds true to its own distinctive character, if separated from the parent species, or if not so separated may interbreed freely with it. But when such interbreeding occurs the offspring fall into two distinct classes, one resembling each parent form. Natural selection now comes into operation to decide, not between one individual and another, but between the two specific forms, that one being favored which is best adapted to its environment, the other being eliminated, or possibly being allowed to survive in a *different* envi-

[1] Verrill, A. E. *The Bermuda Islands.* New Haven, published by the author. 1902, 8vo, x + 548 pp., 38 pls.

[2] Morgan, T. H., *Evolution and Adaptation.* New York, Macmillan, 1903. 8vo, 410 pp.

ronment. Thus mutation may multiply species without necessitating the extinction of any or requiring the erection of barriers spacial or physiological between the new form and the old one to prevent the swamping of the new form by crossbreeding. A real obstacle to the older ideas about evolution has thus been removed by fuller knowledge of the laws of inheritance of mutations.

Though a mutation differs from the parent species at first in a single character only, the number of differences is likely to increase, for one mutation leads to another, as observation clearly shows. Accordingly natural selection is presently called upon to make a choice, not simply between *two* alternative forms, but among several distinct and mutually exclusive types, some one of which will be better adapted to a particular environment than any other.

The adaptations of organisms are almost endless and involve the most minute details of structure and function, yet the two principles of mutation and of exclusive inheritance are sufficient, in Morgan's opinion, to account for them all. Natural selection acting merely on the fluctuating variations of individuals fails to do this.

In justice to Darwin it should be said that the mutation or sport forming tendency of species was distinctly recognized by him, but he attached less importance to the process than do Bateson and deVries. The position taken by these writers, and emphasized by Morgan, is that mutations are the *exclusive* source of the material on which natural selection acts in the production of new species.

A serious defect of the book from the student's standpoint is the total omission of bibliographic references.

W. E. C.

ZOÖLOGY

Zoölogical Investigations in the Malay Archipelago.— Under the auspices of the universities of Edinburgh and of Liverpool, N. Annandale and H. C. Robinson undertook an expedition in 1901–1902 for anthropological and zoölogical investigations in the Malay Archipelago, and some of the zoölogical results of their work have recently appeared in two fascicles.[1] The first contains a report

[1] Annandale, N., and Robinson, H. C. *Fasciculi Malayenses.* Zoölogy. Parts I, II, and Supplement. London. Longmans, Green & Co., 4°, vii + 307 pp., 14 pls.; xliii pp., map.

on the mammals by J. L. Bonhote. In the considerable list of species reported there are a new species of small carnivor, a new bat, a new squirrel, and three new species of rats. C. Swinhoe reports on something over 250 species of moths, of which seventeen are new. Two land planarians, one of which is new, are described by F. F. Laidlaw, who also reports on the dragonflies. Three new diptera pupipara are recorded by Speiser. G. A. Boulenger reports 85 species of batrachians and reptiles, six of which are new. The tiger beetles are described by H. C. Robinson.

The second part contains nine short papers: four on insects, two on fishes, and one each on mollusks, the mouth funnel of a tadpole, and a fossil elephant tooth. In a report on the non-operculate pulmonates W. E. Collinge gives a full account of the anatomy of a new and very large species of Atropos; and in J. Johnstone's paper on the marine fishes, an interesting description of a new species of Periophthalmus is given. Its life on the mud flats out of water and its burrows are fully described and illustrated. The fact that when in the air it does not respond to the report of a gun led to the conclusion that it was absolutely deaf. Its eyesight both in water and in air was acute.

The two fascicles were accompanied by a supplement containing a map and an itinerary.

Davison's Anatomy of the Cat.— As an introduction to the study of zoölogy and particularly to mammalian anatomy, Davison[1] has prepared an account of the anatomy of the cat. The volume, which contains some 250 pages with above 100 illustrations, is unsatisfactorily brief and in consequence it is deficient as a description of the anatomy of a type and as an introduction to comparative study. Although brevity may have been the aim of the author and certain defects may therefore have been unavoidable, others are present in the volume for which no such excuse can be found. Thus the description of the gastrocolic omentum as a *closed* sac is wholly misleading, and the grouping together of the corpora quadrigemina, optic thalami, and corpora striata as basal ganglia counteracts what has been gained for these bodies from the standpoint of comparative anatomy. The facial nerve is placed without qualification among the pure motor nerves, and the circumvallate papillae of the tongue are noted as eight to twelve in number, as in man, though the figure

[1]Davison, A. *Mammalian Anatomy* with special Reference to the Cat. Philadelphia, P. Blakiston's Son & Co., 8°, xii + 250 pp., 108 figs.

shows six, the usual number for the cat. Defects of this kind are too frequent to make the book really useful in the hands of most beginners.

Notes. — The action of light on organisms and the production of light by organisms are presented in readable form by R. Dubois in the second volume of the *Traité de Physique Biologique*. The effect of light on the action of enzymes, on the production and destruction of pigments, and on the circulation and respiration of the higher animal is described at some length. The influence of light on the movements of animals is very inadequately treated probably because most of the researches on this subject have come from other than French laboratories. Dermatophic vision and its relation to vision by means of eyes is fully discussed from the standpoint of Pholas. The production of light by organisms forms a brief, compact essay dealing with the photogenic bacteria, the light-producing protozoa, insects and mollusks. It contains interesting statements of the relative energy values of living and mechanical sources of light and is illustrated by some remarkable photographs taken by light from living organisms. It is marred by an attempt to discriminate between chemical, light, and heat rays.

A brief account of the structure of the rudimentary eyes in the Cuban blind snake, Typhlops lumbricalis, has been published by E. F. Muhse in the *Biological Bulletin*, Vol. V, No. 5, 1903. The eye appears as a dark spot surrounded by an unpigmented circle and covered by a large ocular scale. Internally the usual parts can be distinguished including a well-developed lens and a retina in which the layers typical for snakes can be seen.

R. Dubois last year reported to the French Academy of Sciences and to the Society of Biology the success of his experiment to acclimatize true pearl oysters on the French coast and to produce precious pearls by artificial means. His methods resulted in producing small but high grade pearls in one in ten oysters whereas under natural conditions it was necessary to open 1200 to 1500 oysters to obtain one pearl.

C. H. Eigenmann and C. Kennedy in No. 5, Vol. 4 of the *Biological Bulletin* call attention to an unusual melanic individual of the cave salamander, *Spelerpes maculicaudus*, to a catfish from Lake Titicaca with a branched left barbule, and to a specimen of Xiphorhamphus with an additional left ventral fin.

BOTANY.

The Journals. — *Bulletin of the Torrey Botanical Club*, February: Richards and MacDougal, "Influence of Carbon Monoxide and other Gases upon Plants"; Berry, "Additions to the Flora of the Matawan Formation"; Griffiths, "Concerning some West American Smuts"; Dandeno, "Mechanics of Seed-Dispersion in *Ricinus communis*"; and Howe, "Notes on Bahaman Algæ."

Journal of Mycology, January: — Morgan, "A New Sirothecium"; Hedgcock, "Proof of the Identity of Phoma and Phyllosticta on the Sugar Beet"; Atkinson, "Notes on the Genus Harpochytrium"; Kellerman, "Notes from Mycological Literature" — VIII, and "Index to Uredineous Infection Experiments."

Journal of the New York Botanical Garden, February: — Britton, "George Washington's Palms"; Small, "The Economic Museum"; Nash, "Interesting Plants in Flower in the Conservatories"; Britton, "Botanical Exploration of the Philippine Islands."

Notes. — Two interesting illustrated articles, by Massart, are published in the September *Bulletin du Jardin Botanique de l'État à Bruxelles*, respectively on how perennials maintain their subterranean level, and how young leaves are protected against climatic excesses. The second is illustrated by Ducos-du-Hauron plates in red and blue which give a neutral tint stereoscopic effect when viewed through accompanying red and blue spectacles.

An important paper by Reinke, on "Botanisch-geologische Streifzüge au den Küsten des Herzogtums Schleswig," is published as a complementary heft to Vol. 8, N. F. of the *Wissenschaftliche Meeresuntersuchungen* published by the German Sea Commission of Kiel.

The first part of a study of the plankton of the Illinois River, by Kofoid, published as Article 2 of Vol. 6 of the *Bulletin of the Illinois State Laboratory of Natural History*, forms a quarto volume of xviii + 629 pages, with numerous diagrams and plates.

Adventive bud formation on leaves of *Yucca gloriosa* is noted by Lutz in the *Journal de Botanique* of December.

Nasmith writes on the chemistry of wheat gluten in No. 4 of the Physiological Series of *University of Toronto Studies*.

The association of lime-loving and lime-shunning plants is discussed by Aubert in No. 147 of the *Bulletin de la Société Vaudoise.*

An account of the sex-conditions and hybrids in Ribes, by Janczewski, is separately printed from the *Bulletin International de l'Académie des Sciences de Cracovie*, of December and January.

The rubber-fig of New Caledonia, *Ficus Schlechteri*, is described and figured by Warburg in *Der Tropenpflanzer*, of December.

Cocoa: Its Production and Use, is the title of a paper by Marshall in the *American Journal of Pharmacy*, for February.

An illustrated account of Yerba Mate — *Ilex Paraguayensis*, by Metzger, is contained in *Der Tropenpflanzer*, for January.

A popular article on California mistletoe, *Phoradendron*, with photograms showing its occurrence on various trees, is published by Helen Lukens Jones in *Out West* for February.

An account of useful and interesting plants of the Congo region, by de Wildeman, has been issued from the press of Spineux, of Brussels.

A short sketch of the desert flora about Phœnix, Ariz., by Dams, is published in the *Monatsschrift für Kakteenkunde*, of January.

An account of the useful plants of the Sahara desert, by Dürkop, forms the December number of *Beihefte zum Tropenpflanzer*.

An illustrated account of Samoa and its crops, by Wohltmann, constitutes Heft 1–2 of the *Beihefte zum Tropenpflanzer* of 1904.

A good illustration of a utilized school garden is contained in the 1902–3 *Catalogue of the Boston Normal School.*

A portrait of Professor Farlow forms the frontispiece to *The Popular Science Monthly* of February.

A portrait of Professor Peck is published as frontispiece to Vol. 1 of the *Ohio Mycological Bulletin.*

CORRESPONDENCE.

Editor American Naturalist:

Dear Sir: — Prof. B. G. Wilder has called my attention to errors in nomenclature and typography in my article "Oral Breathing Valves in Teleosts," etc., in the *American Naturalist* for February. The observations recorded in the paper were made two years ago in his laboratory, under the immediate supervision of Instructor H. D. Reed. I supposed that acceptance of the results included sanction of the names employed, whereas it appears that Prof. Wilder and Dr. Reed intended only to commend the observations themselves, and took for granted that, before publication, proof would be submitted to them. My removal to Louisiana rendered this inconvenient; I took for granted that either the manuscript or a proof would be submitted to the ichthyological editor of the *Naturalist*; finally, my own revision had to be done hastily and without access to books. Whatever their causes, the errors are deeply regretted; I realize "the right of scientific names to be correctly written," and avail myself gratefully of the opportunity to publish the following list of corrections.

E. G. Mitchell.

Baton Rouge, La., May 28, 1904.

Page 153, line 5, for Macullum read Macallum.
" " " " " *Amiurus* " *Ameiurus.*
" " " 14, " *Eupomotus* " *Eupomotis.*
" 154, lines 5 and 8, for *brancheostegal* read *branchiostegal.*
" " third line from bottom, for *punctatus* read *gyrinus.*
" " last " for *Eupomotus*, read *Eupomotis.*
" 155, figure 3, second line, for *Clupea*, read *Pomolobus.*
" " " " fourth " " *Astrocopus*, read *Astroscopus.*
" 156 fifth line from bottom, and page 157, 11th line from bottom, *Amblopiytes gruniens*, correctly spelled is *Ambloplites grunniens*, and should be *Aplodinotus grunniens.*

Page 157, figure 7, for *A. gruniens*, read *A. grunniens.*
" 158, for *y-groecum* read *y-graecum.*
" 159, for *Echensis naucratis*, read *Echeneis naucrates.*
" 160, " predacious, read predaceous.
" 161, line 25, for *Amiurus*, read *Ameiurus.*
" " " 28, " *Noturus gyrinus*, read *Schilbeodes gyrinus.*
" " " 29, " *Noturus miurus*, " *Schilbeodes miurus.*
" " " 32, " *Amiurus nebulosis*, read *Ameiurus nebulosus.*
" " sixth line from bottom, for *Amiurus*, read *Ameiurus.*
" 162, 14th " for *Opistheoma*, read *Opisthonema.*
" " 16th " " *Clupea* read *Pomolobus.*
" " 18th " " *Clupea oestivalis*, read *Pomolobus aestivalis.*
" " 19th " " PERCADAE, read PERCIDAE.
" " 21st " " *americanum*, read *flavescens.*
" " 26th " " *Etheostoma*, " *Percina.*
" " 31st " " *Amblopl*y*tes*, " *Ambloplites.*
" " sixth line from bottom, for *Eupomotus*, read *Eupomotis.*
" " last line, for *Apomotus*, read *Apomotis.*
" 163, sixth line, for *auritus*, read *aureus.*
" " 12th " " *Chaenobrytes gulosis*, read *Chaenobryttus gulosus.*

Page 163, 18th line *Apomotus* correctly spelled is *Apomotis*, and should be *Lepomis.*

Page 163, line 26, for *Eupomotus*, read *Eupomotis.*
" 164, " 2, " compareè, read comparée.
" " lines 12 and 15, for Anatomie, read Anatomy.

(*No. 448 was mailed June 16, 1904.*)

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VOL. XXXVIII, NO. 450 JUNE, 1904

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Charles E. Beecher.

THE

AMERICAN NATURALIST.

Vol. XXXVIII. *June, 1904.* No. 450.

CHARLES EMERSON BEECHER.

ROBERT T. JACKSON.

In the death of Professor Beecher the science of Invertebrate Palæontology has lost a most brilliant and eminent leader. In his life so prematurely cut off, he attained a reputation for critical structural and developmental work on fossil animals and philosophical work on the same lines that placed him in the very front rank of his profession.

Charles Emerson Beecher, son of Moses and Emily Emerson Beecher, was born in Dunkirk, New York, October 9th, 1856. He died suddenly of heart disease on February 14th, 1904, in the forty-eighth year of his age. Always a delicate man he had recently been in exceptionally good health, so that his death came without warning. On September 12th, 1894, Professor Beecher married Miss Mary Salome Galligan, who with two young daughters survive him. He left also his mother and a brother, who reside in California.

In his early childhood the family removed to Warren, Pennsylvania, where he attended private and High schools. A born naturalist and collector he in childhood began collecting fossils from the Chemung and Waverly formations about Warren, amassing a choice and extensive collection in that region,

especially valuable for the rare Phyllocarida and for Pelecypoda. He also collected living molluscs and minerals and became well versed in both lines of study. He took the science course at the University of Michigan, receiving the degree of B. S. in 1878.

In 1878 Beecher became assistant to Professor James Hall at Albany, where he remained for ten years. While at Albany he acquired an intimate knowledge of palæozoic fossils, so that with his truly remarkable memory, it seemed that he could name at sight any species offered to him. Always interested in microscopical work he prepared some two hundred and fifty sections of the shells of fossil brachiopods for study in connection with the work of the New York Survey on that group. Besides work on collections of fossils at Albany, he rendered important assistance to Professor James Hall in the preparation of that author's large quarto monographs on cephalous Mollusca,[1] Lamellibranchiata,[2] corals and Bryozoa.[3] As Beecher published little systematic work in later life I would lay stress on what he did as assistant to Professor Hall at this period. To quote Professor Hall, as stated in the Prefaces of the several works cited: "In the preparation and final revision of the descriptions of the species of Cephalopoda I have been very ably assisted by Mr. C. E. Beecher." Again, "In the final revision of the genera and species [of Lamellibranchiata] and in the preparation of the text and the later plates of this volume the author cheerfully acknowledges the very valuable assistance rendered by Mr. Charles E. Beecher." In the second volume on the Lamellibranchiata Professor Hall says: "In the revision of the species, and the publication of this volume, the author acknowledges with great satisfaction the assistance rendered by Mr. C. E. Beecher. In the last work cited on corals and Bryozoa Pro-

[1] *Natural History of New York.* Paleontology. Vol. 5, Part 2, Gasteropoda, Pteropoda, and Cephalopoda of the Upper Helderberg, Hamilton, Portage and Chemung Groups. Albany, 1879. p. 1–15 and 1–492, pl. 1–113.

[2] *Ibid.* Vol. 5, Part 1. Lamellibranchiata [of the Upper Helderberg, Hamilton, Portage and Chemung Groups.] 1, Albany. 1884. p. 1–18 and 1–268, pl. 1–33 and 81–92. 2, Albany, 1885. p. 1–62 and 269–562, 7 figs. pl. 34–80 and 93–96.

[3] *Ibid.* Vol. 6, Corals and Bryozoa .... from the Lower Helderberg, Upper Helderberg and Hamilton Groups. Albany, 1897. p. 1–26 and 1–298, pl. 1–66.

fessor Hall says: "We are indebted to Mr. Charles E. Beecher for the preparation of the synopsis of the genera and sub-genera described and illustrated in this volume; and also for the explanation of plates, with reference to the pages of the volume and the localities of the species." Beecher also assisted Professor Hall in the publication of other works as seen by the texts during his Albany life.

This extensive experience in pure systematic work laid the broadest foundation for Beecher's later developmental and philosophical studies, an experience that is markedly lacking or entirely left out in many who enter into biological problems. It is the expressed opinion of the present Palæontologist of New York State that the influence of Beecher on the palæontology of the State was for the best, and that during his stay of ten years he elevated the standard greatly.

In holidays at Albany he made extensive collections of Unionidæ and other living molluscs in that vicinity. This collection, with the large collections of Recent Mollusca that he gathered at Warren, Pennsylvania, also Michigan, and other localities, previous to going to Albany, he presented to the New York State Museum in 1886 and 1887. According to Mr. Wm. B. Marshall [1] this collection included some twenty thousand specimens and as many more which were considered duplicates, and is almost entirely made up of land and fresh-water shells of the United States, largely collected by Beecher himself. As shown by collating two of Marshall's published papers,[2,3] there are in the Beecher collection at least one hundred and twenty-one species of land and fresh-water Mollusca, mostly from New York and Pennsylvania. One hundred and two localities are represented, seventy of which are in New York State, the others being in various parts of the United States.

Of the species some forty-three belonged to the Unionidæ, a

[1] Marshall, Wm. B. List of Shells Inhabiting the Vicinity of Albany and Troy, N. Y. *48th Ann. Rept. N. Y. State Mus.*, Albany, 1895. Part 1, p. 641–647.

[2] Marshall, Wm. B. Land and Fresh-water Shells of New York exhibited at the World's Columbian Exposition, Chicago, Illinois, 1903. *47th Ann. Rept. N. Y. State Mus. Nat. Hist.*, Albany, 1894. p. 49–75.

[3] Marshall, Wm. B. The Geographical Distribution of New York Unionidæ. *48th Ann. Rept. N. Y. State Mus. Nat. Hist.*, Albany, 1895. Part 1, p. 45–99.

beautiful series of which is on exhibition in the Albany Museum. The collection, which Marshall considered as exhaustive of the vicinity of Albany, is not only rich in species, but very full in series, representing specimens of the same species from various localities and of ages from young to adult. It is therefore very valuable for studies of later development, variation and geographical distribution. As a collection of fine selected material it stands an excellent proof of Beecher's indefatigable industry and appreciation of what a collection should be, much of it, it should be remembered, gathered when he was a youth, or even a child.

In the Albany Museum there are also many minerals and fossils collected by him, and numerous specimens of fossils prepared for exhibition. In free days at Albany he made frequent visits to the rich localities in the Helderberg mountains near Albany, especially Clarksville and Indian Ladder, collecting an extensive series of the fossils to be found there.

At this period Beecher published independently a paper on the Phyllocarida of Warren, Pennsylvania, a number of papers on the lingual dentition of Gastropoda, besides others on recent and fossil Pelecypoda, on geological localities, etc. His most important work was the publishing with Prof. John M. Clarke of a monograph on the development of Silurian Brachiopoda, based on material washed from the clays of Waldron, Indiana. This paper is of importance as the first work on the development of fossil Brachiopoda and opened up new lines of inquiry previously untouched. Always skilful with his pencil, at Albany he added to his income by making drawings for the medical men of that city. Nearly if not all his own papers were illustrated by his own drawings or photographs. During part of his stay at Albany Beecher was Assistant in Palæontology in the New York State Museum, when he did much to develop that department. After he left Albany he was retained for a period as Consulting Palæontologist to the museum, visiting Albany at intervals. Many details concerning his work and connection with the museum will be found in the 32nd to 43rd *Annual Reports of the State Museum.*

In 1888 Beecher went to New Haven as Assistant in Palæon-

tology to take charge of the collections of invertebrate fossils in the Peabody Museum. He took the degree of Ph. D. at Yale in 1889, his thesis being a most interesting monograph on the Brachiospongidæ, of which rare fossil sponges the Yale Museum has a superb series.

Professor Marsh recognized Beecher's ability and his advancement was rapid. To state his official career at New Haven in brief: He was appointed Instructor in Palæontology in 1892, Assistant Professor of Palæontology in 1892, Professor of Historical Geology 1897, and member of the Governing Board of the Sheffield Scientific School in the same year. On the death of Professor Marsh he was in 1899 appointed Curator of the geological collections of the Peabody Museum. In 1902 his title was changed to that of University Professor of Palæontology.

In 1898 Beecher was elected corresponding member of the Boston Society of Natural History, in 1899 member of the National Academy of Sciences, and foreign correspondent of the Geological Society of London. In 1900 he was elected President of the Connecticut Academy of Arts and Sciences, filling that office for two years. While at New Haven he made many trips to western or nearer localities, collecting vertebrate and invertebrate fossils for the museum, and made a trip to Europe with the late Dr. George Baur, visiting museums.

Indian Ladder in the Helderberg Mountains was always a favorite and fertile spot for him, dating back to his Albany days. It is one of the most beautiful and picturesque regions in the Helderbergs. He collected there slabs of limestone containing fossils which were silicified in the most perfect condition for development by etching with acid. From such material he etched numerous large or minute specimens of surpassing beauty and scientific interest. Besides adult fronds of Bryozoa, Brachiopoda, Crustacea, and other fossils in most perfect preservation, he obtained minute embryos and small species in large numbers in literally wonderful condition of perfection. Young Bilobites ½ mm. in length, young Acidaspis .93 mm. in length, and Arges 1.15 mm. long, both of the latter so perfect that he figured them from both the dorsal and ventral view; young Pleurodic-

tyum, consisting of the initial cup alone, and also others with first lateral buds, young Bryozoa showing initial chambers. Such material selected with infinite care and patience formed the basis of a number of papers by Beecher and others. He etched also some very choice fossils from the Hamilton of Canandaigua Lake, New York. One sees and hears so much of poorly preserved fossils, that such exceptionally fine material is refreshing. He made a special point of seeking small and embryonic material by sifting clay from fossiliferous regions with a stream of running water. In this way he obtained choice material from Waldron, Indiana.

In June, 1899, Beecher gave his large and exceedingly valuable collections to the Peabody Museum as he said, "in grateful recognition of the honors and favors conferred upon me during my connection with the University."[1] These collections, made previous to his New Haven appointment, represent the result of twenty years' labor, they were collected wholly by himself and comprised upwards of one hundred thousand specimens, mostly from the Devonian and Lower Carboniferous of New York and Pennsylvania. They contained about five hundred type specimens, published in the *Palæontology of New York*, *Geological Survey of Pennsylvania*, and various scientific periodicals. They also contained hundreds of specimens representing series in development, rare species, and choice specimens exquisitely prepared to show structural detail.

His specimens were always fully labeled as regards locality and identification of genus and species, so that his collections of land and fresh-water molluscs previously mentioned and his collections of fossils represent an immense amount of labor and experience in the field and also in systematic zoölogy and palæozoölogy in working up the collections, and this all as a sideshow to his regular work in official positions.

In his bachelor days at New Haven Beecher with Pirsson, Penfield and Wells roomed in "the attic," the top story of the Sheffield Scientific School, which was comfortably fitted up in true Bohemian style. One of the pleasantest recollections of

[1] *Science*, N. S. Vol. 10. p. 61. July 14, 1899.

visits to New Haven is visits to "the attic" where, after work hours, delightful intercourse, social and scientific was held, often far into the night.

Already interested in studies of the development of organisms from his work noted on the development of Silurian Brachiopoda, in 1889 Beecher became deeply interested in the late Professor Hyatt's methods of work. The application of the principles of stages in development, acceleration, parallelism, and dynamic genesis to the unraveling of the genealogical relations of living and fossil animals. Bringing to this work his large and intimate knowledge of species and the structure of fossil types, Beecher entered into this field with characteristic energy and became the leader of the Hyatt School. Beecher's reputation as an investigator will rest chiefly on the rich results he obtained in the critical, painstaking application of these fruitful principles that Professor Hyatt labored so long to establish.

Already interested in Brachiopoda, Beecher's first application of the Hyatt methods was to this group. Combining the study of young, adult, living and fossil types, he worked out a classification based on the principles of development, and divided the class into four orders. He pointed out the primitive Iphidea from the Lower Cambrian as the archaic radical from which the whole class could be derived. This stands to-day as perhaps the only example in which the primitive radical of a great group equal in systematic value to the Brachiopoda can be pointed out with reasonable assurance. Besides his work on the class as a whole, Beecher wrote many papers in which he worked out the development, structural and genealogical relations of families or minor groups of Brachiopoda. Such are his studies of the development of Bilobites, Terebratalia, Zygospira, and his remarkable studies of loop-bearing Brachiopoda. It is not too much to say that a careful study of Beecher's papers on brachiopods, and the same may be said of his trilobites, will give the student a more comprehensive view of the class than any other published source. Incidentally to his work on the group, Beecher accumulated a rich collection of recent species of Brachiopoda in the Yale museum, illustrating the structure and development, often by large series, in seventy-five species and

five varieties, out of the total known number of one hundred and thirty-eight species and nine varieties of living brachiopods. This statement is taken from a list kindly sent me by Miss Lucy P. Bush, his assistant, who prepared it recently at Professor Beecher's request.

In corals he made important contributions by his beautiful studies of the development of Pleurodictyum and also the structure and development of the zoöids in the colonial form in Michelinia, Favosites and recently in Romingeria.

Thoroughly established in his adopted principles of research, in 1893 he began the publication of his brilliant papers on the structure, development and classification of the Trilobita. Favored by the discovery by W. S. Valiant of Triarthrus in unusual condition of preservation at Rome, New York, Beecher entered into the work. The presence of antennæ had been announced by W. D. Matthew; but Beecher with his marvelous mechanical skill and untiring patience worked out the structure of antennæ, legs and other ventral appendages with a minuteness that had previously been impossible on any known material. His studies of this type made our knowledge of the Trilobita as a class a new thing, putting them on a basis for proper comparative study with other Crustacea. He also took up studies of the development of Trilobita, describing the development in genera in which it was previously unknown or partially known. In 1897 Beecher presented a classification of Trilobita based on his critical studies of young and adult structures together with a consideration of the geological or time sequence, a natural basis for classification as urged by Louis Agassiz and Alpheus Hyatt and nowhere more beautifully carried out than in these trilobite studies. The Trilobita were divided into three orders based principally on the development of the free cheeks. At the time of his death he was at work on an extensive monograph on the structure of trilobites.

In all of Beecher's later work a strong philosophical bent was evinced. This was given full expression in his charming and forceful papers on the origin and significance of spines. In them he urged that spinosity is an expression of growth-force and differential development. The spinose individual or group

of organisms begins as a smooth form, then becomes spinose in a progressively increasing degree until the acme or most elaborate spinosity is attained, then in extreme decadence there is a loss and final disappearance of spinosity, the individual and the group in senility tending to become smooth as in its own early growth. It is a graphic expression of the value of a new conception applied to well known facts.

The student of palæontology has reason to be grateful that many of Beecher's more important papers were combined and published in one volume, *Studies in Evolution*, in the Yale Bicentennial Series, 1901. It is a model of what minute, critical, philosophical palæozoölogical work should be. With characteristic modesty Beecher deplored as extravagance the republication of papers already in print. For the student it is a valuable aid that Beecher's views on Brachiopoda and Trilobita were incorporated in Eastman's translation of Zittel's *Grundzüge der Palæontologie*. The chapter on Brachiopoda being revised by Beecher's intimate friend, Mr. Charles Schuchert, and that on Trilobita being revised by Professor Beecher himself.

Beecher published many other papers besides those alluded to, on Gastropoda, Cephalopoda, and Crustacea, but although interested in stratigraphical and descriptive palæontology he published little in these lines. He published nothing outside of scientific papers as I am informed by Miss Lucy P. Bush. In a review of his papers I find 7 new orders, 1 new family, 2 new subfamilies, 7 new genera, and 20 new species. Most of his papers were brief, that on spinosity being the longest, many of them were combined however in his large work, Studies in Evolution. His bibliography includes some one hundred and eight titles. In addition he wrote a paper, "Extinction of Species," now in press in the *Encyclopædia Americana*, vol. 4. He was for several years an associate editor of this journal.

Being skilled with his hands, ingenious and fertile in mechanical resources, Beecher was an exceptional preparator, as evinced by his remarkable preparations of brachiopods and trilobites, and numerous specimens prepared for exhibition at the Yale University Museum. Especially noteworthy in this direction are the splendid slabs of Crawfordsville crinoids and Cretaceous

Uintacrinus, the huge mount of Brontosaurus and the gigantic yet life-like restoration of Claosaurus, besides numerous individual specimens of invertebrates in all groups. Beecher was a skilful photographer and Professor Hall published[1] his photomicrographs of brachiopod shell structure from slides also prepared by him. Later he published himself photomicrographs of the appendages of Triarthrus, exceptionally difficult subjects. He was a skilful microscopist and made numerous preparations of recent and fossil animals, especially noteworthy are his beautiful preparations of the radulæ of gastropods, sections of shells of brachiopods, sections of corals, sponges, etc. His microscope slides were always the perfection of neatness in finish. One method he adopted is very valuable for appearance and convenience. When sections had to be ground thin he did this on a ground glass slide, when the cover glass was in place the balsam filled the ground surface rendering it transparent, the ground glass forming an attractive border to the slide. This method obviates the necessity of transferring sections to a fresh slide, which is usually done at some risk, for the sake of appearances.

He took great interest in preparing models to illustrate structure, as shown in his models of the development and adult characters of loop-bearing types of brachiopods, his models of Triarthrus showing structure, from the dorsal and ventral view, and his restoration of the huge Devonian crustacean Stylonurus, measuring five feet in length. The details of museum technique also appealed to him strongly, so that he was a most able and successful museum administrator, constantly devising methods to improve the condition and accessibility of collections under his charge. The exhibition rooms of the Yale Museum are a graphic expression of his skill in selecting, preparing and exhibiting collections of fossils.

Beecher was fond of using mechanic's tools and as a relaxation did carpentering and cabinet work at the Museum or at his home. Full of resources he had many interests outside of his technical scientific work.

[1] On the structure of the shell in the Genus Orthis, by James Hall. *36th Ann. Rep't. N. Y. State Mus. Nat. Hist.* 1884. p. 73–75, pl. 3–4.

Quiet, unassuming, modest in a very marked degree, simple, without affectation, entirely free from all eccentricities, conscientious and painstaking in every thing he had to do. In the words of Professor Chittenden, Director of the Sheffield Scientific School[1] "....to those who knew Professor Beecher intimately no words of appreciation will be deemed too extravagant, for close association only brought more clearly to view the many mental traits that testified to the strength of character and of mind that helped to make Professor Beecher one of the strong men of the Scientific School."

Beecher was eminently successful as a teacher, as evinced by the devotion of his pupils and the able papers produced by students under his charge.

Always ready to help with advice, or specimens, he was an appreciative audience, a helpful critic, a warm friend with keen interest in his friends and their work. He will be deeply missed as a friend, and his untimely death deplored as a loss to the science in which he made such a brilliant mark.[2]

[1] Professor Charles E. Beecher. His Life and Work Reviewed [by Miss Lucy P. Bush, not signed]. — Prof. Chittenden's appreciation — Mr. Schuchert's Sketch. [Tribute from a pupil.] *Yale Alumni Weekly.* New Haven, March 2, 1904. Vol. 13, no. 22, p. 487–489.

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VARIATION IN THE RAY FLOWERS OF THE COMMON CONE FLOWER (*RUDBECKIA HIRTA*).

F. C. LUCAS.

The following observations concerning the variation in the ray flower of the common cone-flower or brown-eyed Susan were made during the summer of 1902.

Lot No. 1.— 318 heads. From prairies near what is known as the Stickney tract (Chicago, Ill.). Soil clayey, ground rather moist. Collected July 7th. These heads were picked at random from a large patch. Fig. 1.

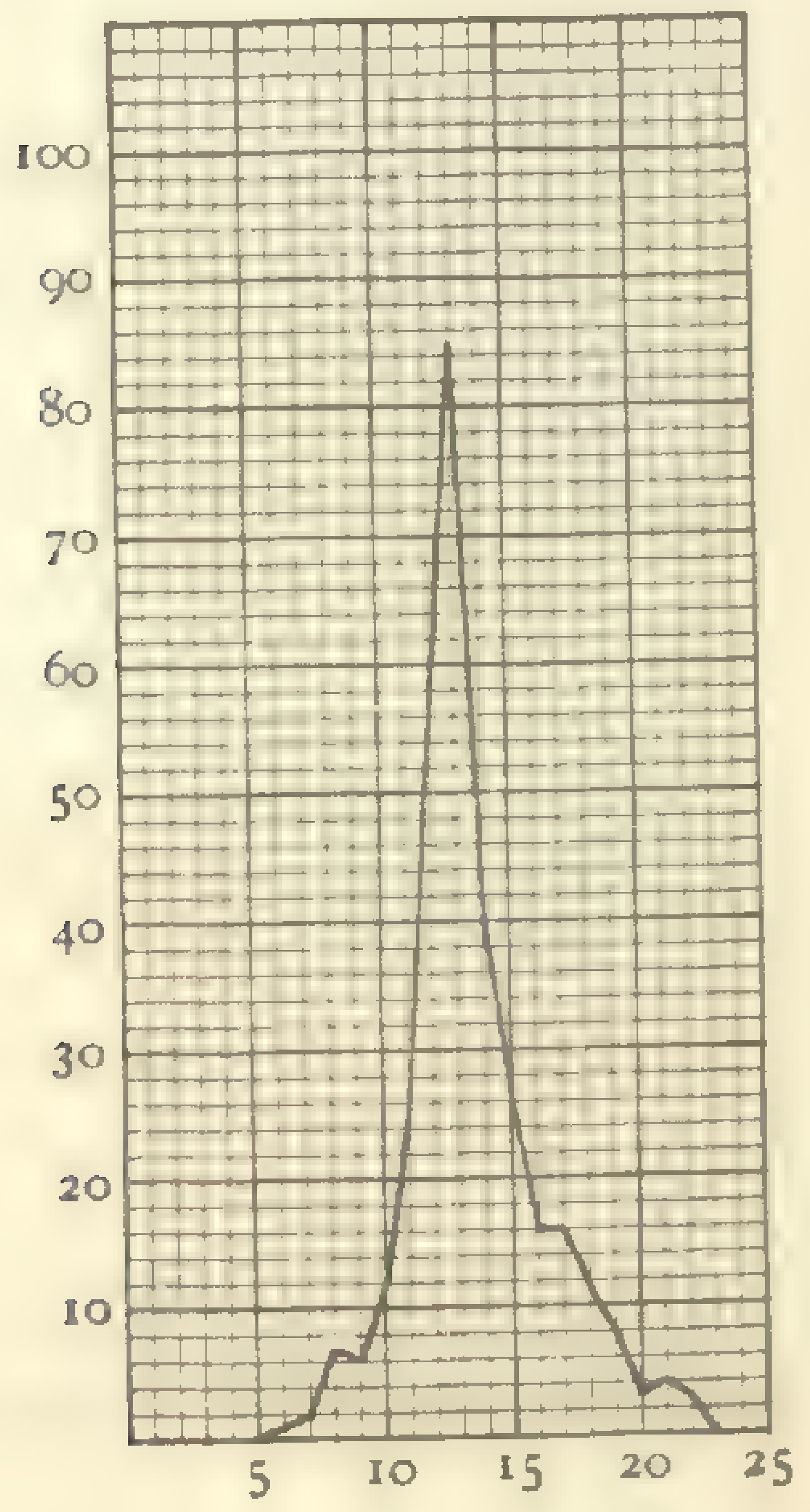

Fig. 1.— Lot No. 1. 318 Heads. Mean — 14, 188 +.

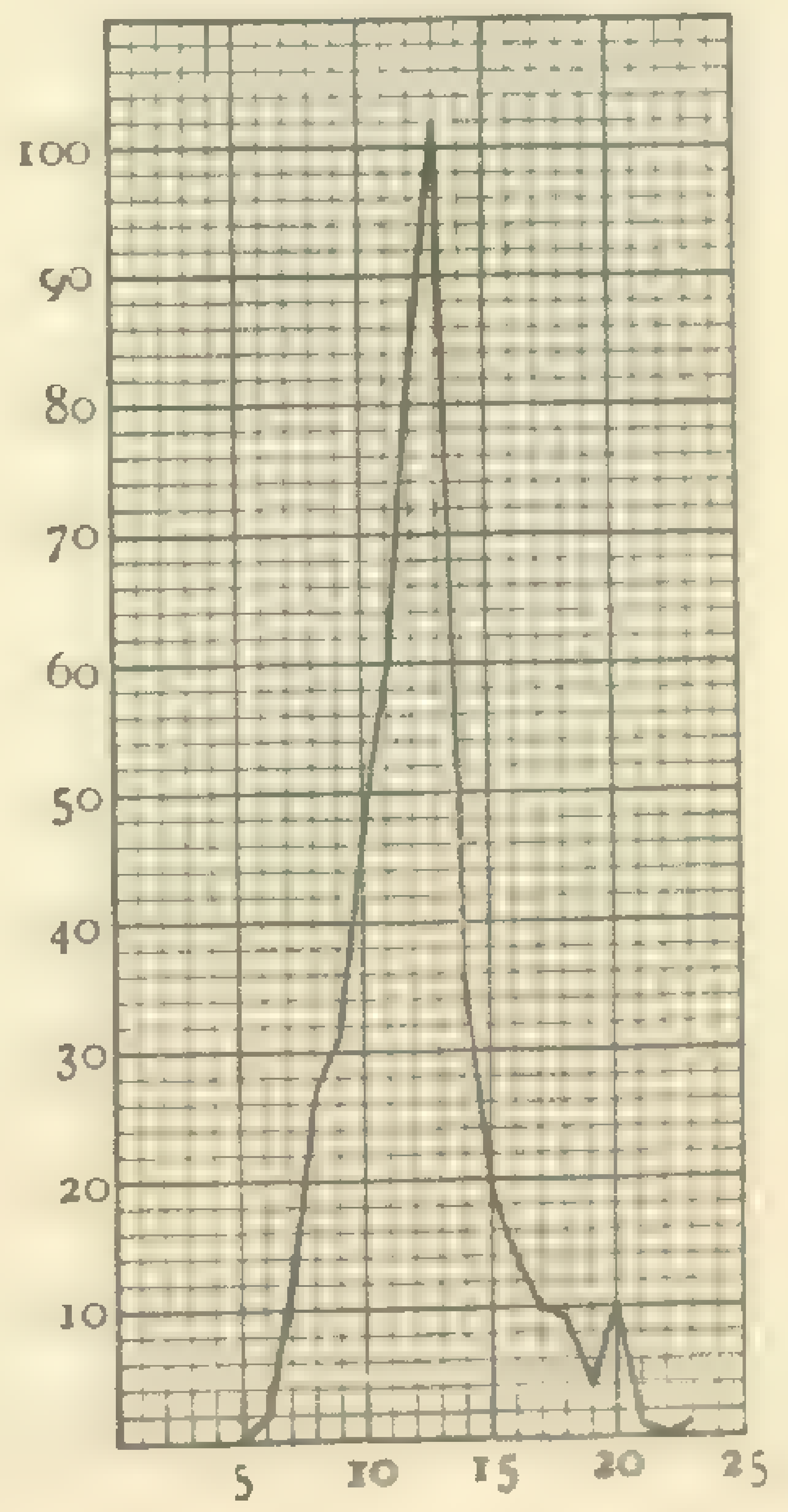

Fig. 2.—Lots 2 and 3. 468 Heads. Mean, Lot 2—11.328 +; Mean, Lot 3 — 11.868 +

Lot No. 2.— 225 heads. Collected from the same region and at the same time as those of lot No. 1. In this case, however, 56 different plants were pulled and all the flowers on each were included in the count. Fig. 2.

Lot No. 3.— 240 heads. From the prairies two miles directly

East of the first locality. Ground was much less moist. 40 plants were collected at random and all the flowers counted as in lot No. 2. Collected July 12th. Fig. 2.

Lot. No. 4.— 173 heads. From the prairies about eight miles southeast of the preceding localities and not far from the lake shore. Ground moist from recent and continued rains. Plants were all rather low and much shaded by tall grass and tall weeds. Collected July 16th. Fig. 3.

Lot No. 5.— 246 heads. From the same general region as

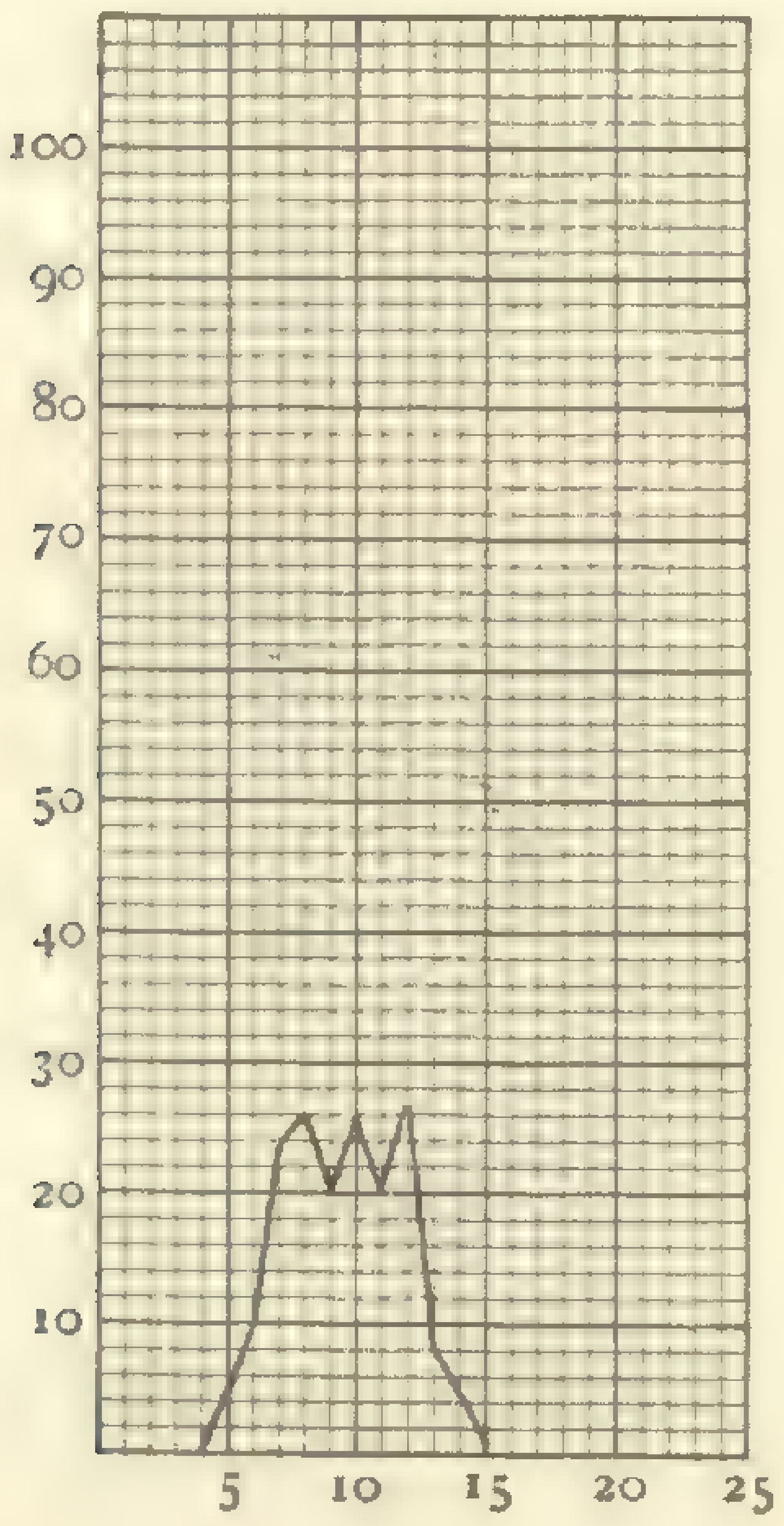

FIG. 3.— Lot No. 4. 173 Heads. Mean — 9.612 +.

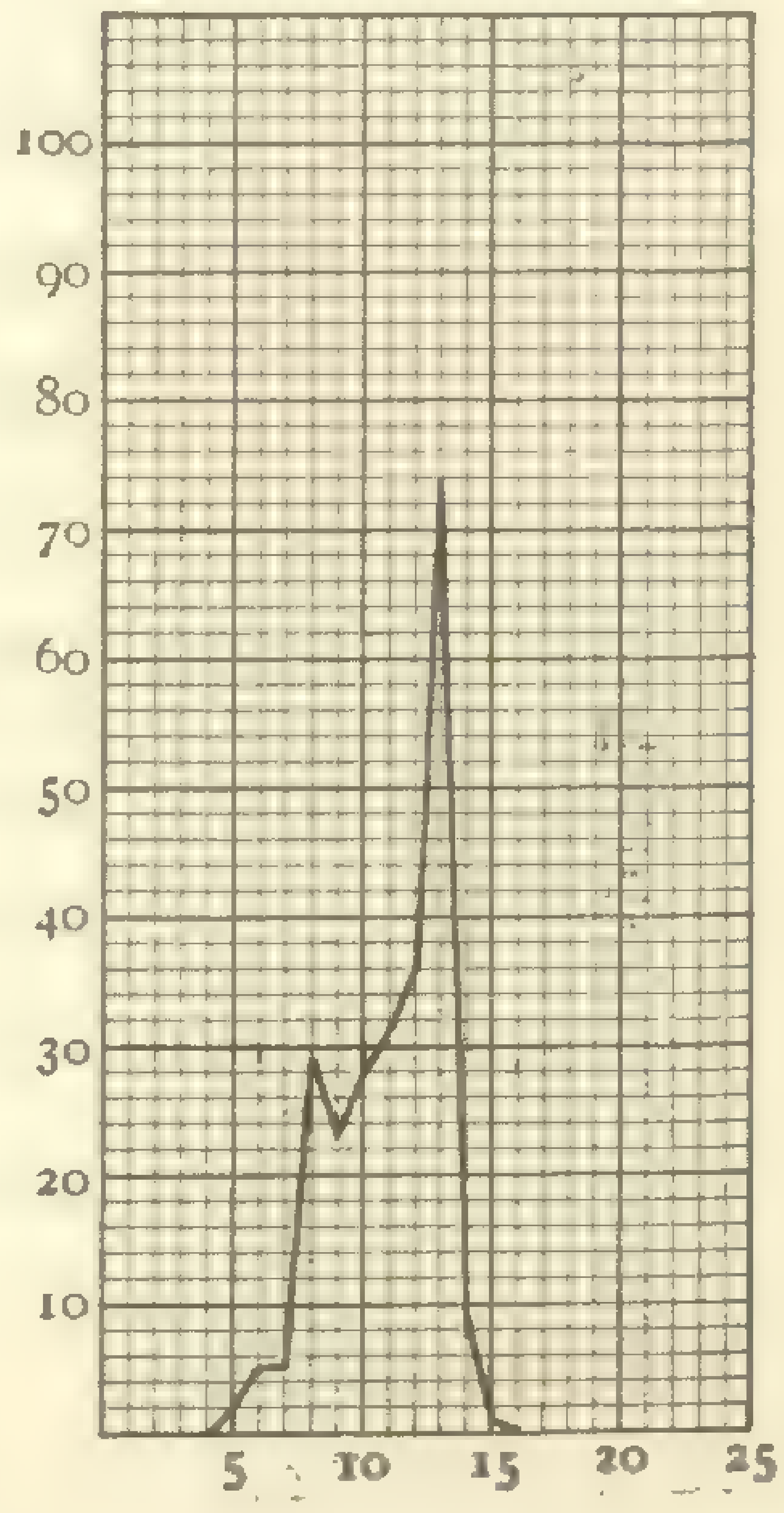

FIG. 4.— Lot No. 5. 246 Heads. Mean — 11.813 +.

in the case of Lot No. 4, but from portions of the prairie where there were fewer weeds and from lanes in the vicinity. Collected July 21st.

In the case of both Lot 4 and Lot 5 plants were pulled up at random and all the flowers of each plant included in the count. The results of the various counts is shown in the following curves.

Comparing the above curves we notice one rather interesting fact. The curve of those heads which were growing under what had been noticed to be especially unfavorable (curve 3) is entirely different from the other three, curves 1 and 2 being especially symmetrical. I am of the opinion that the reason that curve 4 is not so symmetrical as 1 and 2 is that the heads were taken from plants not far enough removed from those represented in

curve 3. The curve in fact shows the transitional condition as regards favorable conditions of growth. Curve 3 on the other hand is a representation in the form of a curve of very unfavorable conditions of growth.

The characteristic mode of *Rudbeckia hirta* is 13. There are also secondary modes at 8 and at 20–21 and the series thus reminds one of Ludwig's series for *Chrysanthemum leucanthemum.* In connection with these different modes it is interesting to note that the number of rays is made the basis of classification.

Species.	Gray.	Britton & Brown.
R. hirta	Rays about 14	Rays 10–20
R. fulgida	Rays about 12	Rays 10–15
R. spathulata	Rays few	Rays 8–12
R. speciosa	Rays numerous	Rays 12–20

ENGLEWOOD HIGH SCHOOL, CHICAGO.

STUDIES ON THE PLANT CELL.—II.

BRADLEY MOORE DAVIS.

THE ACTIVITIES OF THE PLANT CELL.

1. Vegetative Activities.

EVERY cell passes through a history whose events repeat in a broad way activities that have become established in the organism by the experience of its ancestors. The most important of these events is nuclear division, which is accompanied in most plants by cell division, the important exceptions being certain groups whose protoplasm is multinucleate throughout all, or almost all, vegetative conditions (*e. g.*, cœnocytic Algæ and Fungi, plasmodia and multinucleate cells in various tissues).

Protoplasm, whose nuclei can no longer divide, becomes incapable of reproducing itself and must take a dependent position in the organism, where the length of its life will be determined by the good fortune of its environment and its vitality. Such protoplasm becomes strictly vegetative in its functions, and while these activities may be very highly specialized and of the utmost importance to the organism as a whole, nevertheless such a cell has lost certain of the constructive, and in consequence reproductive, possibilities characteristic of living matter. The most evident and important of these constructive activities have to do with the increase of nuclear material (chiefly chromatin), which leads to its distribution through nuclear division, and the development of a complicated mechanism (the spindle) to effect this result.

As Weismann first pointed out, from the standpoint of cell studies, there is a stream of germ plasm flowing with every species, protoplasm relatively fixed in its characteristics and potentially immortal. The chief peculiarities of germ plasm are its reproductive powers and the generalized structure that enables it

to turn to any form of activity possible to the species. Portions of the germ plasm are constantly being detached from the main stream and relegated to more or less special duties. Such protoplasm becomes the body plasm, or soma, of the individual. Specialized body plasm generally loses very shortly the reproductive possibilities of germ plasm, and in consequence must finally die, for its nicely adjusted dependence upon surrounding cells cannot last forever. Yet it has been one of the surprises of biological science that specialized tissues may keep for a very long time the reproductive qualities of germ plasm. Investigations on regeneration in particular have brought these facts conspicuously to the front. As an extreme example among plants, it is known that even the epidermal tissues of leaves and scales of certain ferns (Palisa, :00) may sometimes retain the fundamental qualities of germ plasm and reproduce the plant.

There are no visible characters that separate body plasm from germ plasm, excepting, of course, when body plasm begins to show signs of degeneration. Germ plasm may only be distinguished by its potentialities of growth and reproduction, potentialities that cannot be accurately determined because the stimulus to development is, in the last analysis, an external one and the conditions which govern it may be so intricate as to escape close scrutiny.

Germ plasm is found in its most generalized condition in the cells of growing points, in embryonic and meristematic regions, and in the reproductive tissues. These tissues are well recognized as the most favorable for cell studies because they present most clearly the details of protoplasmic activities. Almost all that we know of cell activities have come from investigations of such regions.

One of the first signs of that specialization which transforms germ plasm to body plasm is the slowing up and final end of nuclear and cell division. With this change come a great variety of modifications (peculiarities of cell wall, plastids, cytoplasmic activities, etc.) which may be readily associated with the particular work of that tissue.

The vegetative activities of germ plasm are chiefly those of growth, which in the end mean reproduction, the embryonic cells

drawing upon food that has been prepared for them and is either stored in special structures (as seeds, spores, bulbs, etc.), or manufactured in differentiated organs or tissues (leaves, chlorophyll bearing tissue, phlœm, etc.). The vegetative activities of body plasm are far more specific than those of germ plasm. Their tissues have particular and highly developed activities, some dealing chiefly with photosynthetic processes, some (phlœm) distributing the organized food over the plant body, some storing the food in large quantities. Besides these there are mechanical functions performed by highly differentiated tissues, even though largely composed of empty cells, as the vascular tissue, supporting tissues, and the external protective integuments.

It is not our purpose to discuss any of these vegetative activities in detail, but only to distinguish as sharply as possible the characteristics of germ plasm with its generalized activities from the specialized body plasm. These generalized characters, as before stated, are constructive activities which mean growth and lead to nuclear and cell division. It is probable that any tissue which presents them has regenerative powers that under the proper environment might be expected to reproduce parts or the entire organism. Germ plasm is distributed more widely throughout the organism than is generally supposed, and many highly specialized tissues still retain the spark of regenerative possibilities. The significance of these conditions is not generally appreciated, perhaps because the environmental conditions of regeneration are little understood and are exceedingly hard to adjust experimentally. There is presented here a very attractive field of botanical investigation, a union of cell studies with the more gross anatomical methods of experimental morphology.

2. Cell Division.

Cell division takes place only after periods of growth that have led to a multiplication of nuclei and in the tissues of plants above the thallophytes is very generally a part of the history of each mitosis. This is because of the structure called the cell plate which is essentially an organ of cell division. But the thallophytes present other methods of cell division which bear no especial relation to nuclear activities, and in certain groups of

the thallophytes nuclear division may proceed through the entire vegetative life of the organism without any segmentation of the protoplasm which only takes place during the reproductive phase of spore formation. But fundamentally protoplasmic segmentation depends on increase in the amount of protoplasm which demands the multiplication of nuclei so that nuclear division always precedes cell division, and we shall consider the events in that order.

(a) Events of Nuclear Division.

1. Direct Division.

The nucleus divides after one or two methods, either directly by constriction or fragmentation, or indirectly (mitosis) when there is present a fibrillar apparatus called the spindle. Direct division is the only form present in the simplest plants and phylogenetically must have preceded the elaborate mechanism demanded for indirect division. This topic will be given especial attention in Section VI. Direct division is also present in certain specialized cells and tissues of higher plants. These are generally old cells or tissues that are far removed from the generalized structure and potentialities of germ plasm. Yet sometimes direct and indirect division occur in the same cell, *e. g.*, Valonia (Fairchild, '94), and such forms might be made the subject of very interesting investigations. In some cases the phenomenon of direct nuclear division accompanies pathological conditions or the degeneration of cells and may take the form of extensive fragmentation. It would be outside of our purpose to discuss such phenomena which is obviously abnormal, and the primitive forms of nuclear division will be taken up later (Section VI). It is possible that direct division in higher plants is in a sense a reversion to early ancestral conditions, a reversion that only comes on when for some reason the normal activities of the germ cell are in abeyance or have ceased.

2. Indirect Division (Mitosis).

Indirect nuclear division, mitosis or karyokinesis, is characterized by a mechanism which varies greatly among plants in its

method of development. The characteristic appearance of this apparatus is a spindle like figure formed of fibrillæ. The poles of the spindle may be occupied by centrosomes or centrospheres or they may be entirely free from such organized kinoplasmic bodies. The essential structures of the spindle are sets of contracting fibers which separate the chromosomes into two groups drawing them to the poles of the spindle where the daughter nuclei are organized. But besides these fibers there are generally present other fibrillæ which complicate the nuclear figure. Some of these extend from pole to pole (spindle fibers) others lie outside of the spindle and end freely in the cytoplasm or attach themselves to chromosomes (mantle fibers), and if centrosomes or centrospheres be present there are likely to be fibers radiating from these centers to form asters.

The events of mitosis are generally grouped into four periods: (a) Prophase, to include the formation of the spindle and preparation of the chromosomes; (b) Metaphase, the separation of the daughter chromosomes; (c) Anaphase, the gathering of the daughter chromosomes into two groups which pass to the poles of the spindle; (d) Telophase, the organization of the daughter nuclei. It is almost needless to say that these periods merge so gradually one into the other that sharp lines cannot be drawn between them. The activities during prophase are especially variable.

Prophase. — There are two types of spindles in plants, (1) those that are formed within the nuclear membrane and (2) those whose fibers originate largely or wholly from kinoplasm outside of the nucleus. Intranuclear spindles have been reported in a number of groups of the thallophytes. They seem to be the rule in the mitoses of oögenesis in the Peronosporales (Wager, '96, :00, Stevens, '99, :01 and :02, Davis, :00, Miyake, :01, Trow, :01, Rosenberg, :03). They are present in Saprolegnia, Fig. 5a (Davis, :03). Fairchild ('94) reports them for Valonia. Farmer and Williams ('98, p. 625) state that the spindle of Ascophyllum is largely intranuclear. Harper (:00) has not described them for the Myxomycetes, but very little is known about the prophases of mitosis in that group and their presence is quite probable. Timberlake (:02) is not positive whether the

spindles of Hydrodictyon are intranuclear or not; they lie in a clear space which, however, may be a vacuole rather than the outline of a nuclear cavity. It seems probable in such a type that the vacuole is really the nuclear cavity whose plasma membrane (nuclear membrane) becomes less clearly defined. The development of the spindle is very difficult to follow among these lower forms because it is so small. Stevens (:03) found an exceptionally favorable type in Synchytrium and came to the conclusion that the spindle developed from the threads of the spirem (linin) entirely within and independent of the nuclear membrane.

Very remarkable intranuclear spindles have been described in the central cell of the pollen tube of Cycas (Ikeno, '98 b) and Zamia, Fig. 5d (Webber, :01). Murrill (:00) found them in the mitosis following the fusion of gamete-nuclei in the egg of Tsuga, Ferguson (:01b) at the same period for pine, and Coker (:03) in Taxodium. They are also reported by Strasburger (:00) in the cells of young anthers and nucelli of the lily and in growing points (Viscum) and possibly may be found quite generally in cells weak in kinoplasmic cytoplasm. The development of the spindles in the above forms has not been studied in detail, but the fibers are probably derived from the linin. We are given a clue to the process by the events of spindle formation in the spore mother cell of Passiflora (Williams, '99). In this angiosperm the nuclear cavity becomes filled with a fibrillar network developed from the linin, the nuclear wall becomes transformed into a mesh connecting the intranuclear fibers with a surrounding cytoplasmic reticulum. The fibers in the central region of this net work develop the spindle which is consequently very largely of intranuclear origin.

Among the thallophytes the poles of intranuclear spindles are frequently occupied by deeply staining bodies which have been called centrosomes; but these structures can hardly be homologous with the well-known centrosomes of other thallophytes, *e. g.*, Stypocaulon (Swingle, '97) and Dictyota (Mottier, :00). They are probably merely temporary accumulations of material with no morphological significance.

Spindles that arise from fibers external to the nucleus (extra

nuclear spindles) are of two main types: (1) those associated with centrosomes, centrospheres or kinoplasmic caps, and (2) those composed of independent fibrillæ developed as a mesh around the nucleus. The latter condition is especially characteristic of the spore mother cell and is perhaps the highest type of spindle formation known for either animals or plants. It is very interesting to trace the relations of this highest condition to the lower types through certain lines of evolution to be discussed in Section VI.

Spindles with centrosomes are known in Sphacelaria, Stypocaulon (Swingle, '97), Dictyota, Fig. 4 *a* (Mottier, :00), the zoösporangium of Hydrodictyon (Timberlake, :02), in certain diatoms (Lauterborn, principal paper '96, Karsten, :00) and in the basidium (Wager, '94 and Maire, :02). The best accounts of the behavior of the centrosomes are given by Swingle and Mottier. Indeed there is much doubt about the history and significance of the bodies in the other forms, although the constancy of their presence at the poles of the spindles indicates that they are really centrosomes. The conditions in the diatoms are especially complicated; an account of Lauterborn's work has been published in English by Rowley, :03. In Stypocaulon, Sphacelaria (Fig. 3 *c*, Section I) and Dictyota (Fig. 4 *a*) the cells studied have permanent asters which lie at the side of the nucleus and which divide just previous to the mitosis and separate so that they come to lie on opposite sides of the nucleus. Fibers develop from the centrosomes on the sides nearest the nucleus and elongating push against the nuclear membrane and finally enter the nuclear cavity to form the spindle.

Spindles with centrospheres are well known in Fucus (Farmer and Williams, '96, '98, Strasburger, '97a), Corallina, Fig. 5 *c*, (Davis, '98), in the ascus, Fig. 5 *b* (Harper, '97 and '99), and in the germinating spore of Pellia, Fig. 4 *c* (Farmer and Reeves, '94, Davis, :01, Chamberlain, :03). Centrospheres have been reported in other forms but the types mentioned above have received the most careful study. It is probable that the centrosphere is but a larger, more generalized kinoplasmic center than the centrosome, a protoplasmic region whose dynamic activities do not focus so sharply as in the latter structure. There are

bodies, as in the basidium, which stand intermediate in size between centrosomes and centrospheres and are probably only called the former because they are very distinct in outline.

Centrospheres in Fucus (Fig. 3 *d*, Section I), Corallina (Fig. 4 *b*) and Pellia (Fig. 3 *e*, Section I, Fig. 4 *c*) are formed *de novo* for each mitosis by an accumulation of kinoplasm at the poles of the elongating nucleus. The centrospheres in the ascus divide before each of the three successive mitoses and finally remain, one for each nucleus, to instigate the peculiar process of free cell formation characteristic of the ascus. Centrospheres are frequently the centers of asters which, however, are usually not as sharply defined as those with centrosomes, possibly because the fibers are not grouped with the same degree of symmetry as is shown around controsomes.

Spindle fibers from centrospheres develop in precisely the same manner as from centrosomes, *i. e.* by the growth of the fibrillæ into the nuclear cavity through the dissolving nuclear membrane. The activity is well shown in the oögonium of Fucus, and Farmer ('98, p. 638) believes "that the intranuclear part of the spindle is differentiated out of nuclear material that is unused for chromosome formation." The entrance of spindle fibers from centrospheres at the ends of a nucleus has been observed by myself in Corallina, Fig. 4 *b* (Davis, '98). The germinating spores of Pellia, Fig. 4 *c* (Davis, :01, Chamberlain, :03) furnish especially good illustrations of the entrance of spindle fibers into the nuclear cavity and the development of the spindle in this form is coincident with the dissolution of the nucleus which, according to Strasburger's theory ('95), indicates that the latter structure contributes material for the growth of spindle fibers.

In connection with the centrosphere mention should be made of the blepharoplasts of the cycads and Ginko which are remarkable bodies with radiating fibers. They have been considered by some as asters with centrosomes, but it is known that they take no part in spindle formation or other mitotic phenomena in these forms, and consequently need not be considered at this time. They will be treated in some detail in the account of the sperm (Section III).

Kinoplasmic caps which form spindles are probably an evolution from the type of centrosphere that is developed *de novo* with each mitosis as in Pellia. Such centrospheres by becoming less definite in form and lacking radiating fibers would be called kinoplasmic caps. Indeed the centrosphere so evident in the early cell divisions of the germinating spore of Pellia becomes a kinoplasmic cap in the later mitoses of the older gametophyte (Davis, :01).

Spindles developed from kinoplasmic caps are characteristic of

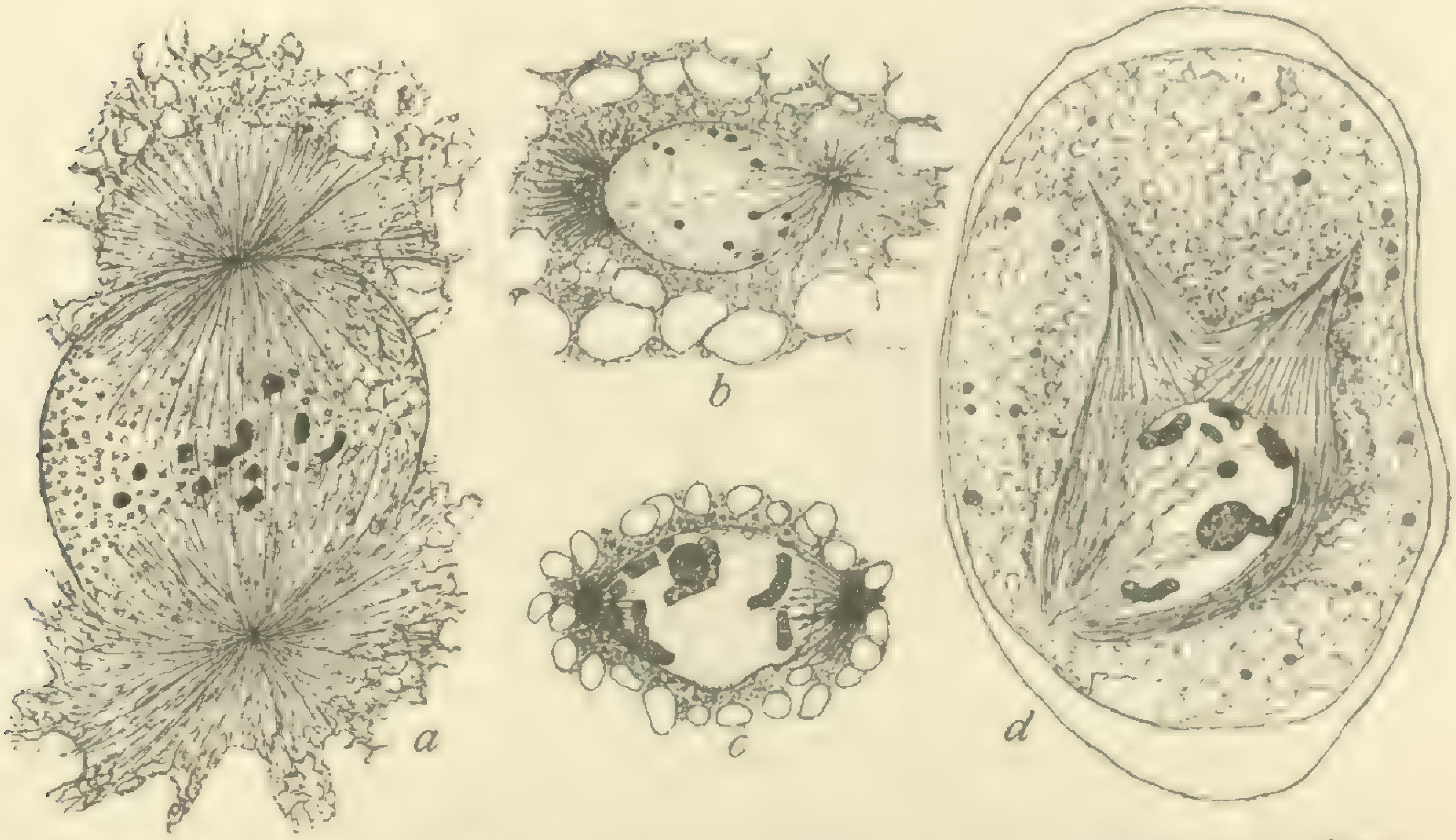

FIG. 4.— Prophases of Mitosis. *a*. Dictyota; late prophase in spore mother cell, fibers from the two asters with centrosomes have entered nuclear cavity to organize the spindle, chromosomes gathering to form the nuclear plate. *b*, Corallina, early prophase in tetra spore mother cell; two centrospheres, the fibers from one having entered the nuclear cavity, chromosomes shown. *c*, Pellia, nucleus in germinating spore; spindle fibers from ill defined centrospheres entering nuclear cavity, chromosomes and a nucleolus present. *d*, Gladiolus, first mitosis in pollen mother cell; a multipolar spindle, nuclear wall breaking down at one side and fibrillæ entering the nuclear cavity, chromosomes and a nucleolus present. After Mottier and Lawson.

the mitoses in vegetative tissues, meristematic and other embryonic regions. They have been especially studied in higher plants by several investigators and for a large number of forms, those most completely described being Psilotum (Rosen, '95), Equisetum, Allium and Solanum (Nemec, '98a and '98b, '99b and '99c), Pteris, Ephedra and Vicia, (Fig. 3 *f*, Section I) (Hof, '98) and Allium (McComb, :00). The polar caps first appear as accumulations of kinoplasm on opposite sides of the nucleus which generally elongates. The protoplasm is granular and although

central bodies have been reported most investigators are agreed that they are only granules without regularity or special significance. They are no longer believed to be centrosomes. Fibrillæ are developed from the kinoplasmic caps and grow out against the nuclear membrane and finally enter the nuclear cavity to form the spindle. A large part of the substance of the kinoplasmic cap is transformed into these spindle fibers.

Papers by Schaffner ('98) on Allium and Fulmer ('98) on the seedling of the pine are the last attempts to bring the centrosome into the history of spindle formation in vegetative tissues of higher plants. But their results cannot stand against the accumulation of studies which indicate that centrosomes are not present in the cells of any plant above the thallophytes with the possible exception of the mysterious blepharoplast and certain structures appearing in some phases in the life history of Hepaticæ. Centrospheres are unquestionably present in the Hepaticæ and centrosomes have also been reported. The centrospheres are, however, so generalized as to approach the kinoplasmic caps in structure and development and it seems quite possible that they are the forerunners of this manifestation of kinoplasm. The so-called centrosomes of the liverworts do not exhibit the specialized structure or behavior of centrosomes among the thallophytes and it is probable that they are only smaller and somewhat more clearly defined centrospheres. These structures in the Hepaticæ seem to hold an intermediate relation between the definite kinoplasmic bodies (asters, centrosomes and centrospheres) of the thallophytes and the remarkable kinoplasmic activities in higher plants which reach their highest expression in the processes of spindle formation in the spore mother cell. These topics will be treated in Section VI.

Structures resembling kinoplasmic caps have been reported in several other tissues than those noted above. Thus Murrill (:00) finds in the formation of the ventral canal cell of Tsuga a dense fibrous accumulation beneath the nucleus which develops one pole of the spindle in essentially the same manner as other polar caps. The other pole of the spindle in this case appears to be formed differently for the fibers seem to be intranuclear.

It would be interesting if two types of spindle formation were present at opposite poles of the same nucleus and further investigation of this subject is much to be desired. The mitoses in the central cell of Pinus (Ferguson, :01b, Chamberlain, '99, and Blackman, '98) and Picea (Miyake :03a) show spindle formation from accumulations of fibrillæ outside of the nucleus but without conspicuous polar caps. Still more striking than the irregular spindle of Murrill in Tsuga, described above, is Miss Ferguson's (:01a) account of the mitosis in the generative cell of the pollen grain of Pinus. The spindle here begins to develop as a cap-like accumulation of kinoplasm below the nucleus. The fibers enter the nuclear cavity and in coöperation with a nuclear reticulum form a system of fibers that extend through the nuclear cavity to the inner side of the nuclear membrane beyond. This portion of the nuclear membrane persists until after metaphase so that one pole of the spindle is found wholly within the nucleus while the other is external and of unquestioned cytoplasmic origin. Coker, :03, regards the spindle which differentiates the nucleus of the ventral canal cell in Taxodium as almost wholly of nuclear origin and the chromosomes as derived largely from the nucleolus. There are evidently some interesting complications in this form which deserve further study.

It should be noted that whenever spindles are formed in connection with centrosomes, centrospheres or kinoplasmic caps that the fibers have a definite region of attachment from which they extend into the nuclear cavity. Such regions constitute a sort of anchorage for the spindle fibers. In this respect the physiological side of the process of spindle formation in these forms is quite similar to that of the animal kingdom and in sharp contrast to other methods that are found in higher plants, which will now be considered.

When spindles are formed after the second method, *i. e.*, by independent fibrillæ making up a network around the nucleus, there is an abrupt change in the method of development. The kinoplasm becomes distributed around the nucleus as an investing layer and shows no inclination to gather into centers such as kinoplasmic caps or centrospheres. There is developed

from this granular kinoplasm a meshwork of fibrillæ that extends into the cytoplasm more or less radially. When the nuclear membrane becomes disorganized the fibers enter the nuclear cavity and organize the spindle (see Fig. 4 *d*). In some forms, *e. g.*, Passiflora (Williams, :00), many or most of the fibers are developed in the interior of the nucleus from the linin and become connected with the extra nuclear reticulum by the dissolution of the nuclear membrane.

The free ends of the fibrillæ that lie in the cytoplasm become gathered into several poles which are distributed variously around the nucleus. This condition constitutes the so-called multipolar spindle (Fig. 3 *g*, Fig. 4 *d*), which in its highest type of development illustrates the most complex method of spindle formation known for animals or plants. During the later periods of prophase the several poles of the multipolar spindle converge and fuse with one another into two poles with a common axis, thus forming the mature bipolar spindle of metaphase (Fig. 5 *f*). The spindle is in a broad sense bipolar, but one may readily see that each pole is made up of several groups of fibrillæ which generally remain quite independent of one another (Fig. 5 *f* 1).

The relation of a multipolar stage to the bipolar spindle of metaphase was first made clear by Belajeff ('94b) for Larix, and later was established more widely by the investigations of Osterhout ('97) on Equisetum, Mottier ('97) for the lily, and Juel ('97) for Hemerocallis. This type of spindle formation is now well known in the spore mother cells of numerous spermatophytes and several pteridophytes. The same conditions in simpler form are found in the spore mother cells of the Hepaticæ, *e. g.*, Anthoceros (Davis, '99), Pellia, Fig. 5 *e* (Davis, :01), and Pallavicinia (Moore, :03). There are a number of very interesting peculiarities in this type of spindle which presents a wide range of variation in the details of its fibrillar organization and development. These will receive special treatment in the account of the spore mother cell (Section III).

The only types of thallophytes known, in which the spindle is partly or wholly of cytoplasmic origin without centrosomes, centrospheres, or kinoplasmic caps, are Chara (Debski, '97) and Spirogyra (Van Wisselingh, :02). The developmental history is

very difficult to follow in these forms and is not fully known, but multipolar conditions are reported which later change into bipolar spindles.

While the spindle is being organized by kinoplasmic activities outside of the nucleus, some events occur within which form a very important part of the prophases of mitosis. The linin material, which in the resting nucleus generally has the form of a net, becomes organized into a much looped ribbon, called the spirem thread. The chromatin material gathers along the spirem thread as deeply staining globular bodies. These split into halves in the direction parallel with the axis of the spirem thread, and the two sets of chromatic bodies lie in two rows along the edge of the ribbon, which shortens as it grows older. Finally the spirem thread divides transversely into a definite number of segments, and these are the chromosomes. The chromosomes are generally fully formed at the time when the spindle fibers enter the nuclear cavity, and they are readily moved as the fibrillæ develop the spindle. Some of the fibers become attached to the chromosomes, carrying them to the equatorial region of the spindle to form the structure called the nuclear plate, which always indicates the approach of metaphase.

As the spirem thread matures the amount of chromatin is greatly increased, so that the separate globules run together and cannot be distinguished in the chromosome which is homogeneous in structure. Chromatin has its greatest staining power at this period. Whether linin is closely related to chromatin in composition and is actually changed into that substance, or whether it dissolves and contributes its material to the growth of the spindle, is a problem of some importance as yet unsolved. It is possible that the nucleolus may furnish material for the chromosomes, and some nucleolar like bodies are known to be chromatic in character, but it does not seem to be established that any of these are genetically related to an unquestioned nucleolus in any plant form.

Important changes come over the nucleolus coincident with the development of the chromosomes. The structure frequently gives signs of internal modifications early in prophase and before the development of the spindle. It may gradually fade away or

decrease in size, or, if large, it may fragment. Strasburger, in 1895, advanced the view that the spindle actually drew upon the substance of the nucleolus for the material and energy necessary to its development. The evidence in support of this suggestive theory lies chiefly in the development of the spindle coincident with the dissolution of the nucleolus. There is also some evidence that the nucleolus contributes material to the developing chromosomes. Small globules, which stain as the substance of the nucleolus, may sometimes be found adhering to the chromosomes as though becoming incorporated in them. These subjects are naturally very difficult of investigation because stain reactions cannot be depended upon with certainty and are not, of course, chemical tests. Then the behavior of the nucleolus during mitosis is exceedingly variable, since it sometimes disappears quickly and sometimes remains intact, and it becomes a very difficult matter to determine its importance. The nucleolus is probably not absolutely necessary at any stage in mitosis, for both spindle fibers and chromosomes develop apart from this structure; but it does seem to be established that the substance of the nucleolus is generally drawn upon by the cell, especially during prophase, when numerous spindle fibers are organized and the amount of chromatin is being largely increased. Experiments of Hottes, which unfortunately have never been published, have an important bearing on these problems.

If the nucleoli are not entirely dissolved they are frequently thrown out of the spindle into the cytoplasm, where they may lie for long periods as deeply staining globules which are sometimes called extra nuclear nucleoli. It is probable that very many of the bodies that pass under this cumbersome title have no relation whatever to the nucleolus. The cytoplasm frequently contains globules that may be coagulated or precipitated food products, and all of these stain similarly to nucleoli.

Metaphase. — The period of mitosis termed metaphase is, to speak precisely, the time when the two halves of the split chromosome separate from one another. However, this is a period of such short duration that for practical purposes nuclei are considered in metaphase when their chromosomes are lined up at the nuclear plate. The metaphase of mitosis is generally the most

conspicuous of the nuclear activities not only on account of the position of the chromosomes (see Fig. 5), but because all kinoplasmic structures (the fibrillæ and centrosomes or centrospheres, if present) are shown to their best advantage.

The best evidence indicates that the chromosomes of plants

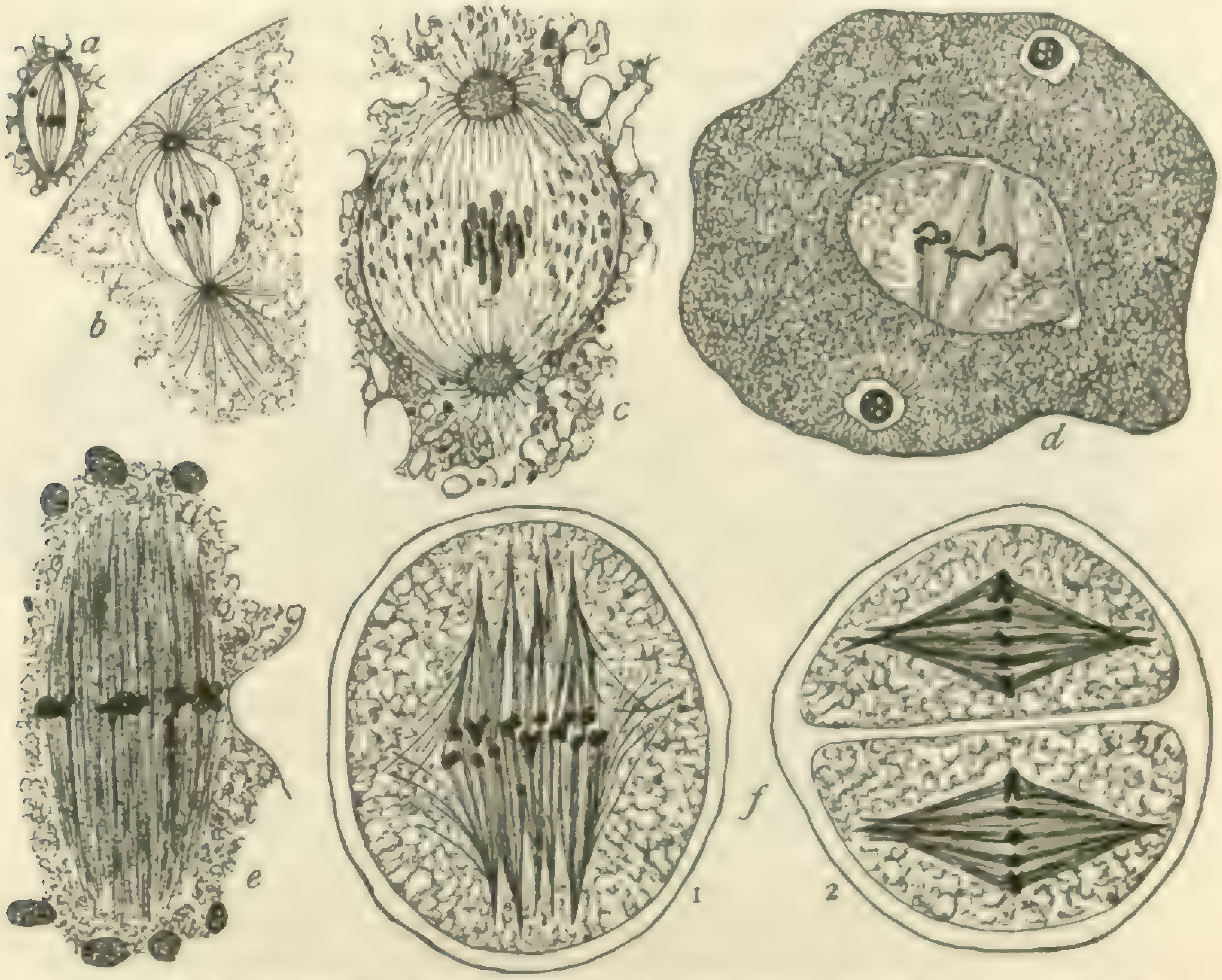

FIG. 5.— Metaphases of Mitosis. *a*, Saprolegnia; intranuclear spindle in oögonium, nucleolus outside of spindle. *b*, Erysiphe; mitosis in ascus, asters with rather smal. centrospheres. *c*, Corallina; first mitosis in tetraspore mother-cell, very large and well differentiated centrospheres. *d*, Zamia; blunt poled intranuclear spindle in central cell of pollen grain; blepharoplasts, their outer membrane about to break up. *e*, Pellia; first mitosis in spore mother-cell: broad spindle with rounded poles, the very numerous spindle fibers ending in granular kinoplasm. *f*, Agave; first and second mitoses in pollen mother-cells: (1), multipolar spindle just previous to metaphase: the several independent cones of fibrillæ gather more closely together to complete the spindle. (2) metaphase of second mitoses: completed spindles showing however the several independent cones of fibrillæ. (After Harper, Webber and Osterhout.)

only divide longitudinally. This matter has considerable theoretical interest, which will be considered in Section V, and also in connection with the spore mother cell (Section III). The daughter chromosomes are drawn apart by the contraction of the fibrillæ to which they are attached.

Chromosomes may take on various forms during metaphase,

especially while they are being separated. Thus, if the chromosomes are dragged apart from the ends, their form is generally rod shaped; but if the attachment of the fibrillæ is near the middle of the chromosome, the structures are pulled apart as loops or V's, and the pair of chromosomes just previous to their separation may be ring shaped. A further complication is introduced in the spore mother cell by certain premature divisions by which each daughter chromosome becomes a pair of granddaughter chromosomes instead of remaining a single structure. The peculiarities of the heterotypic and homotypic mitoses are due

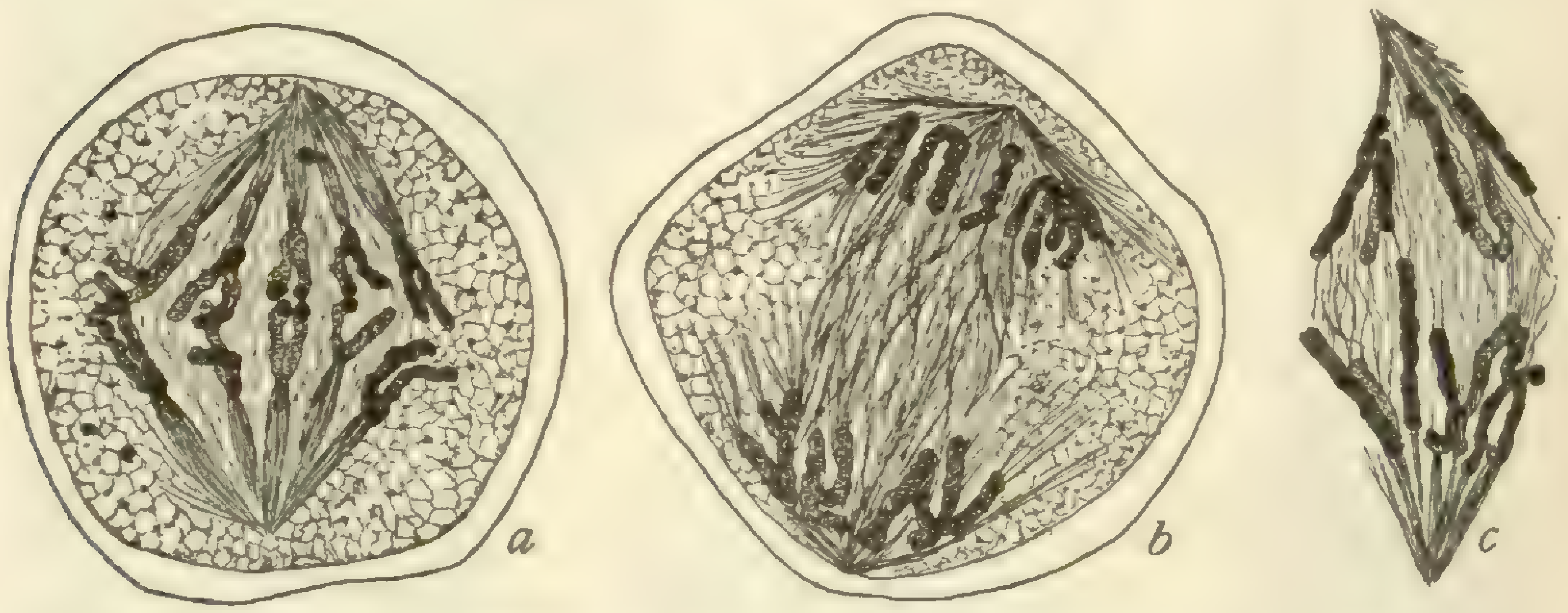

FIG. 6.— Anaphase of Mitosis, spore mother-cell of *Lilium martagon*. *a*, immediately after metaphase of first mitosis; each daughter chromosome consists of two grand daughter segments, adhering at the ends, making the familiar V-shaped figures characteristic of the first mitosis (heterotypic) in the spore mother-cell of higher plants. *b*, late anaphase of the first mitosis; the V shaped chromosomes, each composed of two grand daughter segments adhering at the ends, are very close to the poles of the spindle; the central fibers of the spindle are conspicuous at this stage. *c*, second mitosis; the grand daughter chromosomes, that composed the Vs of the first mitosis, have separated at the nuclear plate of the second mitosis and are being drawn by their ends to the poles of the spindle where they will organize the nuclei of the pollen grain; this mitosis is called homotypic to distinguish it from the usual (typical mitoses in which there are no premature divisions of the chromosomes. All figures after Mottier.

to this phenomenon. (See account of spore mother cell in Section III.

Anaphase.— Anaphase begins with the separation of the daughter chromosomes at the nuclear plate (Fig. 6) and ends with the gathering of these structures at the poles of the spindle preparatory to the organization of the daughter nuclei. As the chromosomes move towards the poles the fibers of the central spindle stand out sharply (see Fig. 6 *b*). If a cell wall is to be formed between the daughter nuclei one may expect to find these fibers thickening in the equatorial region of the

spindle where the nuclear plate formerly lay. Such thickenings are granular accumulations formed by the contraction of the central spindle fibers and mark the beginnings of the cell plate (Fig. 8 *d*) that afterwards gives rise to the cell wall. When the daughter chromosomes reach the poles of the spindle they generally lie in a region of granular kinoplasm which results in part from the contraction of spindle fibers and in some cases from the breaking down of organized centrospheres (*e.g.*, Corallina, Pellia, Fucus, etc.). The daughter nucleus at this time

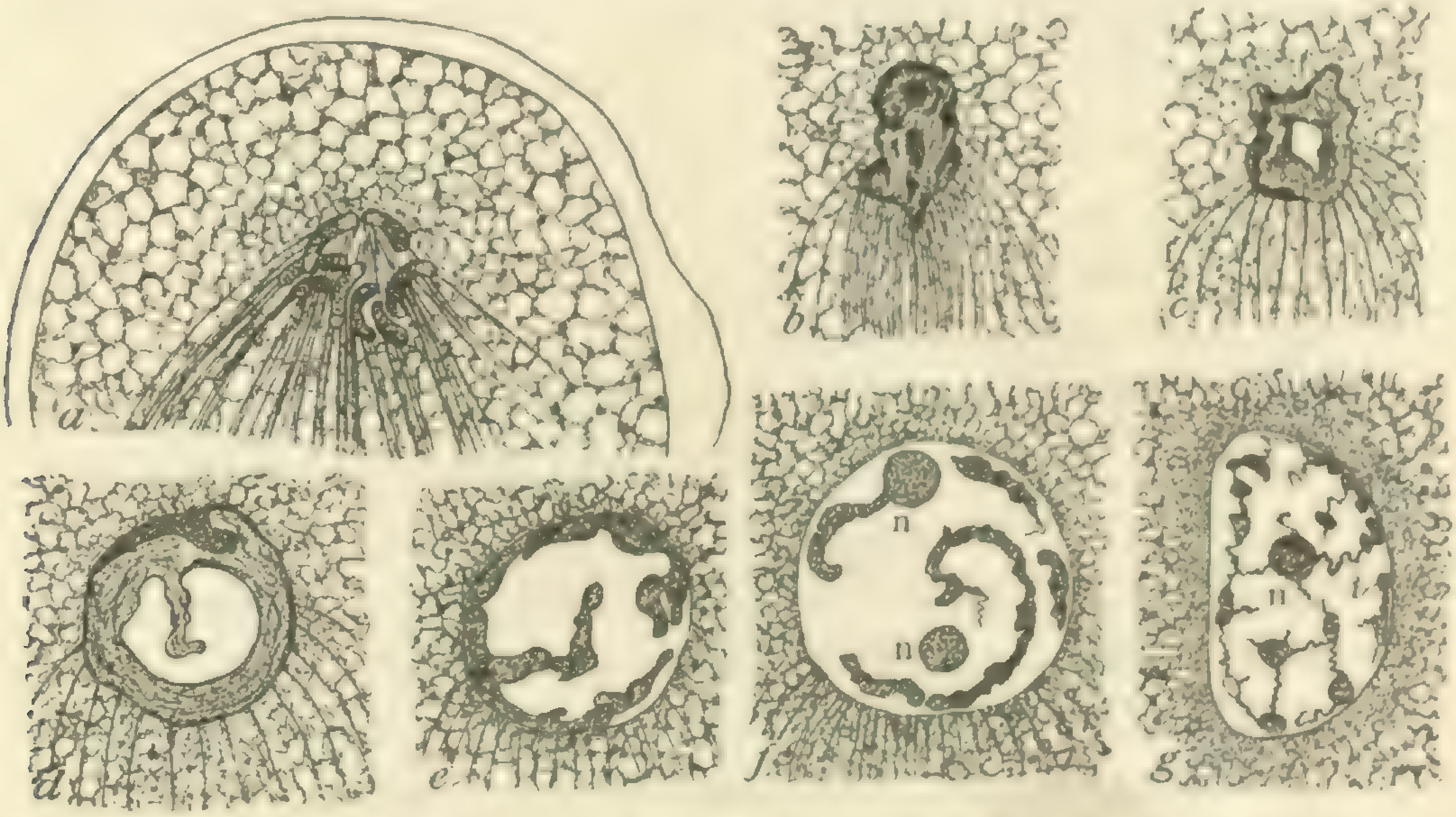

FIG. 7.—Telophase of Mitosis, spore mother-cell of *Passiflora cærulea*. *a*, very late anaphase; the daughter chromosomes are collected at the poles of the spindle. *b*, the commencement of telophase; the chromosomes have fused together and the daughter nucleus is represented by an irregularly shaped mass of chromatin. *c*, the presence of small lacunæ within the mass of chromatin indicates the accumulation of nuclear sap in vacuoles. *d*, an increased amount of nuclear sap, still held however within the mass of chromatin, and consequent enlargement of the vacuole destined to become the nuclear cavity. *e*, the chromatin has begun to break up into small masses so that it no longer holds the nuclear sap which has established contact with the cytoplasm and is forming the nuclear plasma membrane. *f*, nuclear sap in contact on all sides with the cytoplasm and a complete nuclear membrane clearly established; chromatin is very much broken up and two nucleoli (n) have been formed. *g*, the resting nucleus with chromatin distributed in small masses connected by a network of linin threads; a nucleolus (n) is shown; the zone outside the nuclear membrane is kinoplasm and its appearance indicates the approach of the second mitosis in the pollen mother-cell. All figures after Lawson.

(Fig. 7 *a*, *b*) is in its simplest terms, as explained in Section I, a group of chromosomes surrounded by granular kinoplasm and without the nucleolus, linin network or the vacuole which later contains the nuclear sap.

Telophase.—Telophase is the closing period of mitosis and completes the organization of the daughter nuclei (see Fig. 7).

The chromosomes come to lie in a vacuole (Fig. 7 *c*, *d*, *e*) containing nuclear sap and later the chromatin becomes distributed over a linin network and one or more nucleoli develop (Fig. 7 *f*, *g*). As was stated in Section I, the nuclear membrane probably represents the reaction of the granular kinoplasm to a fluid secretion around the chromosomes which becomes the nuclear sap (Lawson, :03a). However, the nuclear membrane is generally a definitely organized film, much more sharply defined than vacuolar membranes. The development of the linin network is not well understood. It is readily seen that the chromosomes become joined end to end and sometimes elongate. The amount of chromatin diminishes as the linin substance appears, but it is not certain whether the chromatin is changed directly into linin, or whether the latter substance is a secretion. The best evidence rather favors the former view. Nucleoli are also believed to hold a very close chemical relation to chromatin.

It is uncertain whether or not the chromosomes lose their organic identity in the daughter nuclei. Investigations on this problem are surrounded by many difficulties. It has been claimed by Guignard ('99) for Naias and Strasburger (:00) for several forms that the chromosomes may be followed with certainty through the period between the first and second mitosis in the spore mother cell. But other investigators have not been able to trace the chromosomes after telophase and are inclined to believe that the chromosome completely loses its identity in the resting nucleus. One of the last investigations of Lilium (Mottier, :03) argues strongly for the latter view, and all who have followed nuclei from one mitosis into another know that the resting nucleus with its linin network and the granular chromatin present conditions that generally make the recognition of chromosomes impossible with the instruments and technique at our command, but this does not prove that they may not be present.

The theory of the permanence of the chromosome has met with much favor because it is argued that otherwise how could the number be maintained so regularly through immense numbers of mitoses. But it can hardly be said that the doctrine is established. It has also found favor because all the events of

mitosis emphasize the importance of the chromosomes which are really the only enduring structures in the nucleus and have led to their being considered as the probable bearers of hereditary qualities.

3. The Dynamics of Nuclear Division.

Mitotic phenomena in certain plant cells present evidence that has very direct bearing on some of the theories that deal with mechanical and dynamical explanations of nuclear division. The methods of spindle formation and the various forms of kinoplasmic structures (centrosomes, centrospheres and kinoplasmic caps) which generally in plants seem not to be permanent organs of the cells all tend to support Strasburger's conception of kinoplasm, which is an outgrowth and application to plants of Boveri's well known theory of archoplasm.

The centrosome theory is supported by very few investigations in Botany, the most notable being that of Swingle ('97), for Stypocaulon, who believes that the centrosome divides with the aster and is maintained as a permanent organ throughout successive cell divisions. Other examples of similar conditions may be found among the thallophytes which, after all, have received very little attention, and such types as Dictyota and the diatoms offer excellent subjects for studies covering a series of cell divisions. But in contrast to Stypocaulon it should be noted that the conspicuous centrospheres of Fucus and Corallina disappear with each mitosis to be formed anew, and the same conditions obtain in the germinating spores of liverworts (Pellia). There seems to be no place for the centrosome in spindle formation as presented in the spore mother cells of all groups above the thallophytes (see Sec. III). Neither does mitosis in the vegetative tissues of these groups, characterized as it is by the presence of kinoplasmic caps, conform to the program of the centrosome theory.

The morphological manifestations of kinoplasm are so various that we are driven to a very general conception of its organization. Kinoplasm runs through cycles in which the structure passes from a granular condition to a fibrillar and then back again

to the granular state. By the granular state we mean one in which no fibrillæ seem to be present, but instead the microsomata are densely and homogeneously massed. It is possible that such microsomata form a closely packed network, but no such structure is visible under the microscope. The first appearance of kinoplasm at prophase of mitosis is frequently the granular condition. This state is illustrated by such accumulations as centrospheres and kinoplasmic caps and by the granular zone that has been reported around the nuclei of some spore mother cells.

Granular kinoplasm becomes fibrillar probably by the arrangement of the microsomata into a reticulum from which fibers extend freely into the surrounding cytoplasm. These fibers undoubtedly elongate during prophase, extending in various directions. Some press against the nuclear membrane and when this breaks down grow rapidly into the nuclear cavity. Of these a portion extend from pole to pole and form the central spindle. Others attach themselves to the chromosomes and lie either among the central fibers or somewhat outside of the spindle (mantle fibers). Still others may extend freely into the cytoplasm as astral rays from the pole of the spindle, a very common condition when centrosomes or centrospheres are present. A contraction of the fibrillæ, beginning with metaphase, is just as characteristic of mitosis as their elongation during prophase. The fibers attached to the chromosomes draw the latter to the poles of the spindle. The central fibers in higher plants draw away from the poles and give their substance to the cell plate. The substance of contracted mantle fibers, with other kinoplasm at the poles of the spindle, probably become distributed around the group of daughter chromosomes so that they finally lie surrounded by a sphere of kinoplasm.

It does not seem as if we knew much more about the structure and activities of kinoplasm during mitosis than is indicated in this cycle of change from a granular condition through a fibrillar state back to the granular condition, with a period when the fibers elongate and another when they contract. This with few exceptions is the history for every mitosis. The exceptions deal with peculiar conditions or structures. Thus, for example,

the astral rays of the centrospheres in the ascus instead of contracting to a center or disappearing in the cytoplasm after the last mitosis grow around the nucleus and cut out a portion of the cytoplasm to form the spores, thus contributing their substance to a plasma membrane.

There is little doubt that kinoplasmic fibrillæ actually exist as structural elements in the protoplasm. Their growth and movement in the cytoplasm and nuclear cavity, their multiplication and shifting arrangements as the spindle develops, and their contraction to the poles of the spindle or to a cell plate give these fibers an individuality that cannot be explained on the theory that they merely represent lines of force or paths of dynamic stimuli. They apparently perform all the activities mentioned above by virtue of their own structural organization which is that of rows of microsomata and in this organization resemble and are probably closely related to cilia. There is an excellent discussion of this subject by Allen, :03, p. 302, etc.

Some authors believe that there is a streaming movement in the astral rays (Chamberlain, :03, for Pellia) either towards or away from the pole of the spindle. This view is founded on the granular appearance of the radiations which are sometimes very thick in Pellia and enlarge at the points where they join the centrospheres or the outer plasma membrane. It is not altogether clear that the larger of these structures are quite the same as spindle fibers since they seem to be actually strands of cytoplasm rather than fibrillæ.

It is probably safe to assume that the forms which kinoplasm takes have relation to dynamic activities, but it is not easy to define these. Thus centrosomes, centrospheres and kinoplasmic caps may well be the centers from which dynamic stimuli extend, and they may be the focal points of other energies. These problems have been very little investigated among plants. It is obvious that differentiated regions of kinoplasm have important physical relations to other portions of the protoplasm, one of the most important being the anchorage which they give to fibrillæ, thereby largely governing the direction of such strains as come about through the contraction of these structures in the later periods of mitosis.

But the essential characteristics of kinoplasm stand out sharply from whatever point the phenomena of mitosis is viewed, and in this protoplasm with its power of forming contractile fibers is vested some of the most conspicuous activities of nuclear division as well as the important powers given plasma membranes in relation to the segmentation of protoplasm to be considered presently.

The dynamic activities concerned with the spindle present only half the story of mitosis. The other important events occur inside of the nucleus. One of these is the dissolution of a portion or the whole of the nucleolus which takes place as the spindle develops and we have already given the views of Strasburger ('95 and :00), supported by the studies of other investigators, that its substance in certain instances furnishes material for the development of the spindle. But the chief events in the interior of the nucleus deal with the accumulation of chromatin on the spirem thread which with the disappearance of the linin indicates that the latter substance may become converted into the former. The splitting of the spirem ribbon longitudinally is of the utmost significance for thereby is made possible an exact and homogeneous distribution of the chromatic material in the nucleus. We do not know how the spirem ribbon splits nor have we as yet any evidence of the origin and evolution of this peculiar activity.

(b) Segmentation of the Protoplasm.

Mitosis in the uninucleate cells of plants is generally followed by immediate cell division, which takes place in groups above the thallophytes through the formation and *cleavage of the cell plate* in the equatorial region of the spindle between the daughter nuclei. Among thallophytes, as so far studied, cell division is chiefly through *cleavage by constriction*. There are forms among the thallophytes and also in the spermatophytes whose nuclei gather about themselves a portion of the cytoplasm, wherein they lie, which becomes cut out of the general mass by a cell wall. This is *free cell formation.*

Multinucleate masses of protoplasm, such as plasmodia and

portions of cœnocytes, generally divide extensively at reproductive periods and always through *cleavage by constriction* with, however, the frequent coöperation of vacuoles which help to cut the protoplasm in the same manner as the cleavage furrows. *Cleavage by constriction* is undoubtedly the most primitive type: *free cell formation* and *cleavage by cell plates* being special and very highly developed protoplasmic activities.

1. Cleavage by Constriction.

A simple example of *cleavage by constriction* is presented by such an alga as Cladophora. The process consists in the building out of a ring of cellulose from the side wall into the cell cavity. The outer plasma membrane forms a fold, thus placing the two surfaces opposite one another (see Fig. 8 *a*), and the wall is laid down between these. Spirogyra forms its wall in precisely the same manner as Cladophora with this peculiarity, that the new wall finally cuts through the protoplasmic strands that connect the daughter nuclei. These strands are said to contain spindle fibers (Van Wisselingh, :02) which may contribute to the plasma membranes forming the cell wall, as it is completed. Another illustration of *cleavage by constriction* is presented in the formation of gametes of moulds (Sporodinia) and the abstriction of conidia (Erysipheæ), both processes having been studied by Harper, '99, p. 506. In these cases a cleavage furrow proceeds from the surface inward and divides the protoplasm. The partition wall of cellulose is formed later between the two free plasma surfaces. The only differences between the processes above described are that in the first forms the cleavage proceeds more slowly and the wall follows the furrow as it progresses in the interior of the cell, while in the latter types cleavage is complete before the plasma membranes develop the wall. Cell division in the red Algæ (Rhodophyceæ) is also a process of constriction similar to Cladophora, but the wall is not generally formed entirely across the filament so that adjacent cells remain connected by thick strands of protoplasm.

These processes become much more complicated when large masses of multinucleate protoplasm are divided up into many

smaller bodies as during spore formation among the Myxomycetes and Mucorales. Very complete studies have been made of these conditions by Harper, '99 and :00 a. In the slime mould (Fuligo) cleavage begins by furrows on the external surface which "cut down at all angles into the homogeneous protoplasm." The direction of the cleavage furrows is further complicated by the fact that many of them start from the bottom and sides of deep folds. All of the furrows may bend and secondary cleavage planes strike off from them which in time unite with one another until the protoplasm is divided progressively into very many small masses (see Fig. 8 *b*) that finally round themselves off and secrete walls, becoming spores, sometimes with one nucleus and sometimes with several.

Cleavage in the sporangium of Synchytrium and the moulds, as described by Harper, '99, is in general similar to that in the plasmodium with, however, the additional feature that lines or planes of vacuoles are often utilized to assist a cleavage furrow in effecting the segmentation of the protoplasm. The separation of the spore plasm of the sporangium of Pilobolus from the filament below begins with a cleavage furrow from the exterior; but this furrow follows and makes use of a curved plane of flattened vacuoles with the result that a dome shaped cleft is developed and two plasma membranes are presented face to face, which form the columella wall between them. The segmentation of the spore plasm in Pilobolus is affected somewhat similarly through the coöperation of cleavage furrows from the exterior with vacuoles which cut into the protoplasm at various angles to meet one another and the cleavage furrows. The bodies first formed in the sporangium of Pilobolus are not the final spores. Harper suggests that they may correspond to the zoöspores of Saprolegnia. They are generally uninucleate and begin immediately a period of growth within the sporangium characterized by extensive nuclear multiplication and several divisions of the protoplasmic body by constriction.

Harper finds that the spore plasm of Sporodinia is separated from the filament below by a dome-shaped plane of flattened vacuoles which fuse together and, unlike Pilobolus, cut their way to the surface of the sporangium. Thus the cleavage is deter-

mined entirely by the activity of vacuoles. Spore formation, however, is accomplished by cleavage furrows which progress from the exterior inwards and, without the aid of conspicuous vacuoles, cut out multinucleate masses of protoplasm which become the spores.

Dean Swingle (:03) has extended the studies of Harper on spore formation in the molds to Rhizopus and Phycomyces. He confirms Harper's account of the general processes of cleavage by furrows coöperating with vacuoles, and notes the following characteristics in the types studied. In Rhizopus the position of the columella is determined by a dome-shaped series of flattened vacuoles which fuse and meet a cleft that extends upward from the outer plasma membrane at the base of the sporangium. The spores are formed in Rhizopus by branching systems of curved furrows that cut the protoplasm into multinucleate masses, and in Phycomyces by angular vacuoles that develop into furrows which extend in various directions and unite with one another and with clefts from the region of the columella.

Other excellent illustrations of *cleavage by constriction* are presented in the sporangia of such types as Hydrodictyon, Cladophora and Saprolegnia. Timberlake (:02) has given an account of Hydrodictyon, and the events are also fairly well understood for Saprolegnia. Segmentation begins in Hydrodictyon by the development of cleavage furrows in the outer plasma membrane, which cut into the protoplasmic layer at right angles to the surface and meet similar furrows that make their way from the large central vacuole outward. These cleavage planes spread laterally, uniting with one another, until the protoplasm is all divided into uninucleate masses which become the zoöspores (Fig. 8 *c*). In Saprolegnia (see Davis, :03, for general account) conspicuous cleavage furrows develop from the central vacuole and make their way to the exterior, finally breaking through the outer plasma membrane. When this takes place there is an immediate escape of cell sap, which was under pressure, and a shrinkage of the sporangium so that the zoöspore origins appear to fuse, but this is not really the case, for cleavage is continued and the zoöspores soon separate.

A physiological explanation of *cleavage by constriction* must

consider two sets of factors. There is an evident contraction of the protoplasm in many examples because water is given off. The shrinkage of the surface would undoubtedly form furrows, but, as Harper has pointed out, these furrows do not develop in an accidental manner. Non-nucleated masses of protoplasm are never separated from the nucleated, but the segmentation proceeds after a system by which the final products contain only one nucleus or at most a limited number. So it is probable that the nuclei are the ultimate centers controlling the segmentation which at its commencement may be quite irregular. This explanation of sporogenesis in the plasmodium and the sporangium is not altogether satisfactory for the cell division of Cladophora, the abstriction of conidia or the development of the gametes of a mould. In these examples the cleavage begins at definite regions of the plasma membrane, so that the stimulus must be local, and the direction of the plane has a definite relation to the axis of the plant.

It is important to note (see Harper, :00, p. 240–249) how inadequate are some of the well-known theories of the segmentation of protoplasm as explanations of *cleavage by constriction.* Hofmeister's law ('67) that cell division is across the axis of growth obviously cannot be applied to the irregular segmentation in the plasmodium and sporangium, nor is Sachs' well-known law of growth in vegetative points adequate. Sachs, '94, and in the *Lectures on the Physiology of Plants*, chap. XXVII, conceives a growing point of a higher plant or an embryonic structure as a mass of protoplasm whose cell walls are determined by principles of rectangular intersection of perpendicular planes. The outer form of the structure determines the angles of periclines and anticlines and the transversals conform to these. There is not the slightest hint of such an order in the distribution of cleavage planes in the multinucleate masses of protoplasm just described and Sachs' law in so far fails of general application whether or not it be satisfactory for the conditions with which he especially deals. There are also explanations of cell division, applicable to the tissues of many higher organisms, based on the position of the nuclear figure in the cell, which determines the position of the cell plate but these theories cannot handle the events in the

plasmodium or sporangium where the cleavage planes are formed without regard to the time of nuclear division or the position of mitotic figures.

2. Cleavage by Cell Plates.

Cleavage of the protoplasm by means of the cell plate is almost universal in cell division of plants above the thallophytes. It is one of the peculiarities of plant cells, having been found in comparatively few animals and there represented rather imperfectly by the so-called mid-body. The general events of the process have been known since Treubs' studies of 1878, and were clearly described by Strasburger in 1880. Timberlake, :00, in a recent paper gives an historical review of the subject.

When, after the metaphase of mitosis, the two sets of daughter chromosomes separate from one another there is left between them the spindle, made up of the central fibers. The first appearance of the cell plate is a line of granules in the equatorial region of this spindle where the nuclear plate formerly lay. But several important events proceed this condition. The connecting central fibers begin to thicken, first near the daughter nuclei, and then gradually towards the equatorial region of the spindle. The number of fibers may increase greatly, probably by the separation of bundles of fibrillæ composing the spindle into independent elements (Timberlake, :00, p. 94). But there is evidence that new fibrillæ are sometimes formed from the vicinity of the daughter nuclei, some of which may enter the spindle and coöperate with the connecting fibers. In certain forms (*e. g.* Allium) there is an accumulation of a stainable substance between the connecting fibers in the equatorial region of the spindle. The reaction of this substance to stains indicates a carbohydrate composition.

The cell plate really begins with the thickening of the connecting fibers in the equatorial plane of the spindle. In some forms these thickenings are elongated bodies, in others mere granules. The earlier writers (Treub, '78, Zacharias, '88) did not believe that they came from the spindle fibers, but there seems to be now no doubt of their origin from these elements,

which contract and thicken as the plate develops. The bodies composing the cell plate finally lie in a plane extending the entire width of the spindle (Fig. 8 *d*) and they then broaden and come in contact with one another to form a continuous membrane, which, as has been said, may lie in a matrix of carbohydrate material. The cell plate grows rapidly as the central spindle fibers shorten and contribute their substance to the structure. During this contraction the surrounding cytoplasm

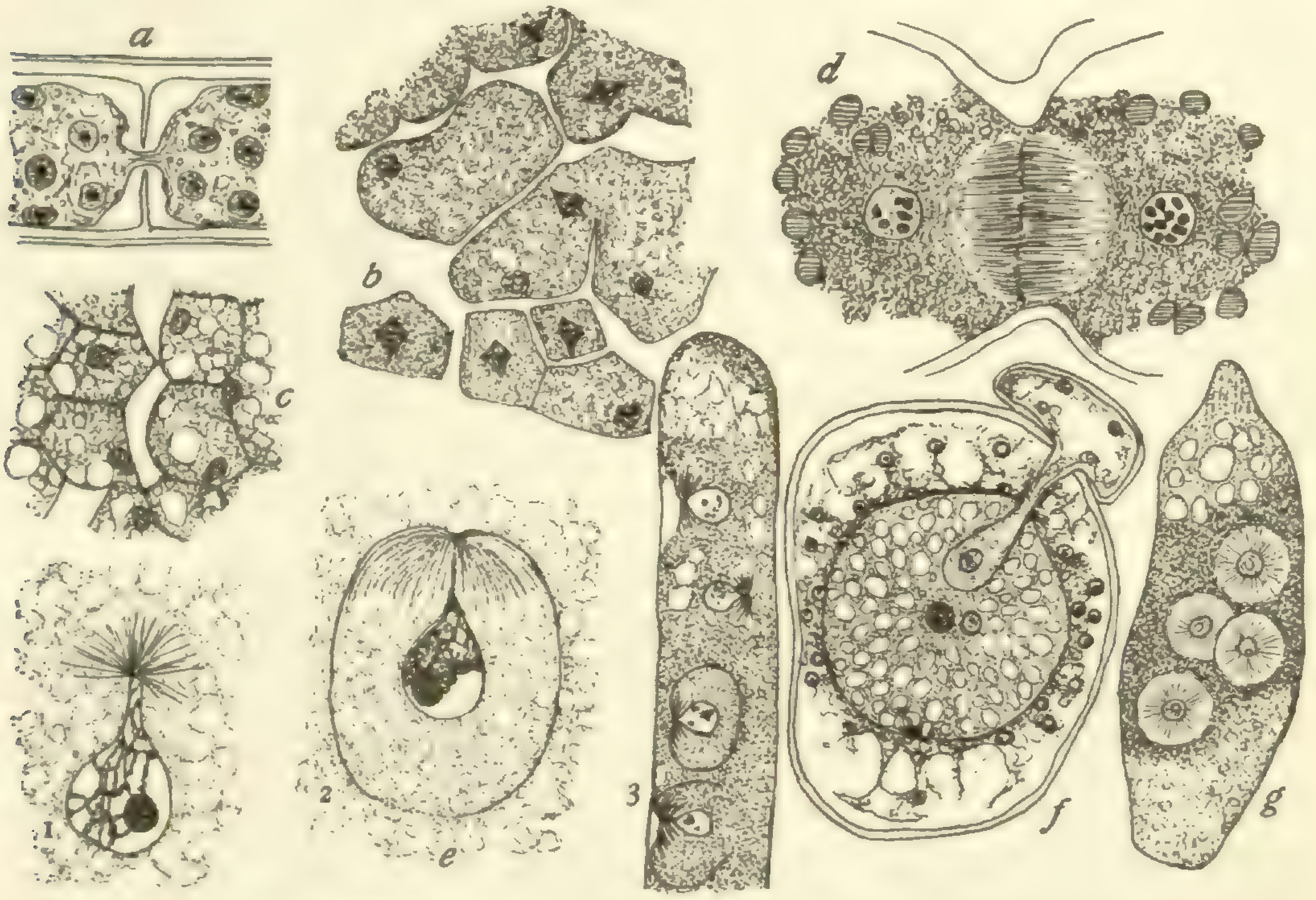

Fig. 8.—Segmentation of the Protoplasm. *a*, *b*, *c*, cleavage by constriction. *d*, cleavage by cell plate. *e*, *f*, *g*, free Cell Formation. *a*, cell division in Cladophora. *b*, cleavage of spore plasm in Fuligo. *c*, spore formation in Hydrodictyon. *d*, first division of spore mother-cell in Pellia. *e*, spore formation in ascus, 1 and 2 (Erysiphæ) astral fibers cutting out cytoplasm around nuclei, 3 portion of ascus with developing spores (Lachnea). *f*, oögonium of Albugo, egg surrounded by membrane pierced by antheridial tube, cœnocentrum and female gamete nucleus within. *g*, egg of Ephedra with four embryo cells. After Strasburger Harper and Timberlake.

enters the region between the barrel shaped group of fibers and the daughter nuclei (Fig. 8 *d*). It is probable that the cell plate is composed entirely of the substance of spindle fibers and in consequence is kinoplasmic in character. The cell plate widens with the accretion of material from the central spindle, which in some cases is assisted by the radiating fibers that, lying outside of the spindle, contract and add their material to the edge of the plate. The cell plate thus extends laterally and finally reaches

the neighboring cell walls, fusing with the outer plasma membrane. There are certain mitoses, as in some spore mother cells and in the embryo sac (see Section III) where the cell plates are absorbed into the cytoplasm leaving the original cell with two or more nuclei and without partition walls. It is uncertain whether the edge of the plate is ever extended by the development of additional peripheral fibrillæ (Timberlake, :00, p. 161) from the daughter nuclei.

Cell division is accomplished by the splitting of the cell plate (Strasburger, '98) into two plasma membranes. The division generally begins in the center and the cleft progresses towards the periphery until it reaches the cell wall. During the process the thickened rod shaped portions of the spindle fibers are pulled apart. There are thus left two kinoplasmic membranes opposite one another and continuous with the outer plasma membrane surrounding the daughter cells. The cause of this cleavage is not apparent, but there are reasons for believing that the split is essentially a thin vacuole which, starting near the center, cuts its way through the cell plate to the periphery after a manner very similar to the behavior of vacuoles during the cleavage of the plasmodium and in the sporangia of certain moulds. And there may be shown in this activity a relationship of *cleavage by cell plate* to some of the events of *cleavage by constriction*. After division is complete there follows the formation of a cell wall between the two cell surfaces after the method usual to plasma membranes.

The new cell wall generally begins in the oldest portion of the cell plate where the cleft first appeared and is gradually built out peripherally until it reaches the side walls. The first indication of the wall is the appearance in the cleft of a stainable carbohydrate substance which resembles the material that was primarily present between the fibers of the central spindle and which disappears with the formation of the cell plate. This material is probably the basis of the first deposits on the surface of the two plasma membranes, but the nature of the final substance is exceedingly various. A cell wall may be formed that is homogeneous throughout but often the thickened wall presents three regions, two layers of a cellulose basis formed by the

respective plasma membranes and between them the so-called middle lamella.

The middle lamella has been the subject of much discussion. It is not the remains of the cell plate as was once supposed. Neither is it exactly a cement between two cell walls. Its history is undoubtedly various, for the composition shows much plasticity. The origin of the middle lamella at the surface of a plasma membrane indicates a morphology similar to a cell wall, but the substance, pectic in character, shows transformations far removed from the cellulose compounds that are formed later and which give thickness to the cell wall. Allen (:01) discusses the subject in detail.

The origin of the cell plate is a subject of interest which will be further discussed in Section VI. There are some types, especially among the thallophytes, where a cell plate is present, but apparently in a somewhat undeveloped and rudimentary condition. These forms suggest transitional conditions between *cleavage by constriction with the aid of vacuoles*, so general among the thallophytes, and *cleavage by the cell plate*, characteristic of higher groups. The most interesting examples are Anthoceros, Chara, Basidiobolus, Pelvetia, Fucus, and Sphacelaria.

Cell plates are formed with each of the two successive mitoses in the spore mother cell of Anthoceros (Van Hook, :00; Davis, :01, p. 158), but the structure in some species is exceedingly small (*e. g.*, *A. lævis*) and can scarcely extend more than one-tenth of the distance across the cell. It is larger in other forms, as in the one studied by Van Hook; but even there the nuclear figure of the second mitosis is only one-third of the width of the cell. The protoplasm divides simultaneously in the four spores with the characteristic arrangement. If this division were determined entirely by cell plates there would be required an extensive development of fibrillæ, of which there is no evidence in the cell. But their place seems to be taken by numerous delicate strands of cytoplasm which connect the four protoplasmic masses, each of which contains a large chromatophore and an accompanying nucleus. A film is formed in the intermediate region, and this marks the position of the cell wall. It is, of course, quite certain that the two cell plates of the second mitosis are

a part of this membrane and may start its development, but the final structure must contain very much more material than could possibly be contributed by the sparsely developed spindle fibers. Thus, although the splitting of the cell plate may start the process of segmentation, its final course and end is probably determined by cleavage through vacuoles, thus utilizing a method characteristic of the thallophytes.

Chara appears to have a fairly well developed cell plate (Debski, '97) which extends almost entirely across the cell, presenting very exceptional conditions among the thallophytes. This peculiarity is in keeping with other characters of the spindle, which begins its development outside of the nuclear membrane and, lacking centrosomes, resembles the nuclear figures of higher plants. It is possible that nuclear studies upon Chara throughout ontogeny might show a variation that would be very significant for the evolutionary problems concerned with the structure of protoplasm.

Fairchild ('97) reports a cell plate for Basidiobolus when the beak cells are cut off from the gametes. The structure, as figured and described, is not, however, conspicuous. He points out general resemblances between cell division in this form and in the Conjugales, where, as Van Wisselingh (:02) described later for Spirogyra, spindle fibers connect the daughter nuclei and may coöperate towards the end of cell division with a cleavage furrow from the side of the cell.

The conditions in the Fucales are not altogether clear. Both Strasburger ('97a) and Farmer and Williams ('98) report that the central spindle disappears in Fucus without the formation of the cell plate and that the wall is developed between the daughter nuclei in a region of granular cytoplasm. However, in Pelvetia some of the radiating fibrillæ from opposite sides of the daughter nuclei bend around these structures and end in the new wall. It is not plain that they contribute much if anything to its formation in the way of substance, but it would seem probable that they hold a directive relation to the structure (Farmer and Williams, '98).

The Sphacelariaceæ seem to be somewhat similar to the Fucales in their methods of cell division. The beautiful figures of

Swingle ('97) for Stypocaulon give details of the region of the cytoplasm that forms the partition wall between the daughter nuclei. There is a zone of fine meshed protoplasm between much larger vacuoles. It is possible that some very long fibrillæ may connect the daughter nuclei with this zone, but they do not form a cell plate. Consequently the wall must be developed in this delicate alveolar layer, which probably splits along some plane of vacuoles. The process of cleavage is then really related to such activities of vacuoles as occur in the sporangium of the Mucorales and in the plasmodium. But the position of the alveolar layer may be determined by the fibrillæ, since it is always situated nearest to the smaller of the two daughter nuclei.

It seems likely that the process of cleavage in the Fucales will be found to be similar to Stypocaulon when the details of structure in the internuclear cytoplasm is known. So this group, with others, is likely to furnish conditions in which spindle fibers may determine the position of the cell wall and exert a directive influence upon it without actually laying down a cell plate. As has been pointed out, the splitting of the cell plate is probably a cleavage along a very thin flat vacuole, so that the process in its essential characters is the same as cleavage through a series of vacuoles. Thus *cleavage by the cell plate* is possibly an outgrowth from that phase of *cleavage by constriction* in which the extensive fusion of vacuoles determines the planes of separation. The important advance lies in the new factors, introduced through the activities of fibrillæ, which become very conspicuous as actual contributors of material to the kinoplasmic film which is laid down as the cell plate. This function of the fibrillæ probably developed slowly from conditions such as those in Stypocaulon and Pelvetia, where their influence upon the position of the cell wall, if any at all, can scarcely be more than directive.

3. Free Cell Formation.

Whenever a nucleus becomes the center around which cytoplasm is gathered and separated from the rest of the cell contents, so that the new cell lies freely in the protoplasm of the old, this is *free cell formation*. Illustrations are presented by

the spores of an ascus, the oöspore of the Peronosporales, the embryo cells of Ephedra, and probably other gymnosperms, and in some cases seemed to be exemplified in the conditions presented by the egg and synergids and the antipodals of the embryo sac.

Spore formation in the ascus is known through the studies of Harper ('97 and '99). After the final divisions in the ascus the nuclei lie in the cytoplasm, each with an aster at its side (Fig. 8 *e*, 3). A delicate prolongation carries the aster with its centrosphere away from the main body of the nucleus (*e*, 1). The rays of the aster now bend over and grow around the nucleus, presenting an umbrella-like figure (*e*, 2). They finally meet on the opposite side, and thereby cut out a portion of the cytoplasm which is included in the spore. The substance of the aster fibers forms the basis of a kinoplasmic film which becomes the plasma membrane of the ascospore and develops the spore wall externally after the usual method. This peculiar activity of an aster is unparalleled in plant or animal cells.

Oögenesis in the Peronosporales has been described in some detail by several authors, but the process has not generally been called *free cell formation*. Yet at the end of the process the oöspore, enveloped by periplasm, lies free in the oögonium. In the beginning the oöplasm gathers in the center of the oögonium as a denser alveolar region around that peculiar protoplasmic body (generally present) the cœnocentrum. This accumulation forces the vacuoles, together with most of the nuclei, to the periphery, where they lie in a sort of protoplasmic froth next the cell wall and constitute the periplasm. The spore wall develops at the boundary of the oöplasm, so that it lies close to the large vacuoles (Fig. 8 *f*) in the periplasm. There must be an accumulation of kinoplasm, perhaps from the plasma membranes of numerous vacuoles, to form a delicate layer between the two regions of the oögonium. This layer of kinoplasm probably splits along the line of vacuoles between the oöplasm and periplasm, for the primary walls are certainly established between two plasma membranes, because the secondary layers are added to it from both sides. Nuclei in division frequently lie very close to the boundary of the oöplasm, but there is no evidence

that the kinoplasmic membrane has any relation to these mitotic figures. That is to say, there are no fibrillæ to contribute substance to the membrane, and its development must be concerned with vacuoles alone. In this respect the process recalls the part played by vacuoles in the plasmodium and in certain sporangia during cleavage by constriction.

Free cell formation after the method in the egg of Ephedra (Strasburger, '79), which is also likely to be found among other gymnosperms, takes place during the differentiation of the embryo cells. The cytoplasm collects around each nucleus, forming a sphere (Fig. 8 *g*), and a wall is developed on the outside of this body. Details of the process are not known, and it is not clear whether the position of the membrane is determined by the vacuoles that must border upon this region or whether there are fibers radiating from the nucleus which might lay down a cell plate around the denser protoplasm; but the evidence favors the former possibility.

Somewhat similar conditions are presented in the egg apparatus of many embryo sacs. In certain forms (*e. g.*, the lily so well described by Mottier, '98) the egg nucleus and synergids are thickly invested by radiating fibers, and these, together with the cell plates, may readily determine the position of the plasma membrane that forms the cell wall. But fibers do not seem to be conspicuously present in the egg apparatus of many other embryo sacs (Excellent illustrations can be found among the Ranunculaceæ). In these cases the protoplasm collects around the nuclei as dense areas bordered by vacuolar cytoplasm, and it is possible that the vacuoles by fusing with one another cut out these respective regions and thus determine the plasma membranes of the egg and synergids. Such processes would extend the activities of vacuoles, which accompany cleavage by constriction in the thallophytes, to the highest groups of plants.

It is curious that with all of the work upon the embryo sac we should know less about the segmentation of the protoplasm around the synergid, antipodal, and segmentation nuclei in this structure than in the sporangia of the molds, the ascus, or during spore formation in the Myxomycetes.

(*To be continued*).

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NOTES AND LITERATURE.

ZOÖLOGY.

Notes on Recent Fish Literature.— In the *Transactions of the Liverpool Biological Society* (XVII, 1903) Mr. Walter M. Tattersall takes up again the classification of the lancelets in connection with the study of Professor Herdman's collection from Ceylon.

Tattersall recognizes about 12 species, with two or three marked "varieties." These he arranges under two generic heads, Branchiostoma and Asymmetron. As a synonym of Asymmetron (1893) he places Epigonichthys (1876). The last mentioned name has of course priority over Asymmetron, if the two are identical. "Subgenera" Tattersall proposes to "abolish altogether" because most of those proposed contain but a single species; an inadequate reason for those who mark divergence of character rather than number of species, by the use of subgeneric names. Mr. Tattersall regards the American *B. caribæum* as identical with *B. lanceolatum* of Europe, which conclusion is not unlikely, as the only difference known is the usually smaller number of post-anal muscular impressions in the American form (9 or 10 instead of 10, 11, 12 or 13). The Japanese Lancelet (*B. japonicum* = *B. nakagawæ*) is the same as the Ceylon species, *B. belcheri*, and that again is indistinguishable from the European. It has 63 or 64 muscular impressions while *B. lanceolatum* has 60 to 63 and *B. caribæum* 58 to 61. The averages of specimens counted indicate a slight increase in number of segments in Asiatic specimens, a slight decrease in American.

Tattersall rejects the genus Amphioxides, based on *A. pelagicus* and characterized by the absence of oral cirri "because the absence of oral cirri is no doubt a result of its pelagic life." But if pelagic life brings about such important structural modifications, a matter by no means proved, this is no reason why we should not regard these modifications as of generic value. If Amphioxides is really without cirri, as is probably the case, it is surely a valid genus.

Mr. Tattersall states that "Jordan and Snyder consider *B. nakagawæ* a new species solely on account of its geographical distribution." In this he seems to miss the point. *B. belcheri* was described from Borneo in very unsatisfactory fashion. The Japanese lancelet showed

points of difference. As in almost every case, the shore fishes of Japan are specifically different from their analogues in Borneo, it is antecedently probable that the lancelets differ also. It appears that this is not the case, as a correct account of *B. belcheri* agrees substantially with *B. nakagawæ* (earlier called *japonicum*). Yet Mr. Tattersall finds a certain average difference. The commonest formula of myotomes in *B. belcheri* is 37–17–9, while in *B. japonicum* it is 36–17–11. As these little creatures have so few tangible characters, minute differences which can be made out have a greater relative importance.

In the *Bulletin of the Museum of Comparative Zoölogy* (Vol. 39, No. 8) Mr. Samuel Garman gives an account of the fishes taken by Mr. Alexander Agassiz and his party on the "Albatross," about the coral reefs of Fiji and the great Barrier Reef of Australia. Fourteen new species are described and well figured, nearly all of them from Fiji.

In the *Bulletin of the Fish Commission* (1903), Dr. Oliver P. Jenkins gives a final account of the splendid collection of fishes made by him in Hawaii in 1889. Two hundred fifty-four species are included in this connection, and in this and two preceding papers ninety-three species are described as new. The fauna of Hawaii is essentially that of the tropical Pacific. The same genera occur as in the other islands, but not all the genera. Many of the types characteristic of the south seas, as Periophthalmus, Synancidium, Variola, Terapon, Cæsia, never reach Hawaii. A large percentage of the species of Hawaii are peculiar to that archipelago. Thus although Hawaii, like other groups of Islands, has Scari, Holocentri, Gobies, etc., it has its own species in these groups, for the most part unlike those found in Samoa or Tahiti. The faunal isolation of Hawaii may be due in part to the direction of the currents, which set to the westward, while at Samoa their general direction is eastward. The new genera in Jenkins' paper are Scaridea, Cirrhitoidea, Eviota, Chlamydes, the last two being gobies. The excellent plates in this paper are by Mr. William S. Atkinson.

In the *Proceedings of the U. S. National Museum* (XXVI, 1903), Dr. Gill takes up Dr. Boulenger's studies of the bones of the Opah, *Lampris luna*. Dr. Gill makes a very different interpretation of the osteology of the shoulder girdle from that of Dr. Boulenger. He finds the so-called infraclavicle to be the hypocoracoid, and believes that the bones of the Opah differ little from those of the related

mackerel-like fishes. He finds no warrant in associating the Opah with the sticklebacks to form a group Catosteomi. The present writer agrees fully with Dr. Gill in his view of this matter.

In the *Proceedings of the U. S. National Museum* (XXVI, 1903), Dr. Gill discusses the generic names in a forgotten work of Heinrich Friedrich Linck, 1790. "Versuch einer Eintheilung der Fische nach der Zähnen" in "Magazin für das Neueste aus der Physik und Naturgeschickte," published at Gotha. The paper is without value, but some of its generic names antedate those in common use. These are Mustelus for *Mustelus lævis* = *Squalus mustelus*. This antedates the use of the name for *Mustelus canis*, for which Dr. Gill suggests the new group name, Cynias. Pristis and Mola of Linck are equivalent to the genera later so named by Latham and Cuvier. The other new generic names are Rhinobatos (without type indicated), Callichthys (no type), Alosa (no type), Thymallus (no type), Soarus (definition unintelligible), Barbatula (= Cobitis).

Gill further shows that the name Macrodon Schinz (1822) was intended for the genus of Sciænoid fishes called Ancylodon by Cuvier in 1817, preoccupied by Ancylodon Illiger 1811, and later named Sagenichthys by Berg. The type of the Sciænoid genus should, therefore, stand as *Macrodon ancylodon*.

For the genus of Erythrinidæ called Macrodon by Müller in 1842, Gill substitutes the name Hoplias.

He further calls attention to the fact that Oken in 1817 (in *Isis*) gave classical names to the genera of fishes left with French names only by Cuvier in the first edition of the Règne Animal of the same year. From this work, the following names must date: Monacanthus, Alutera, Triacanthus, Curimatus, Piabucus, Cirrhinus, Bagre, Lota, Brosme (not Brosmius, a later form), Monochirus, Aurata, Plectropomus, Priacanthus, Stellifer, Sander (= Lucioperca), Zingel, Otolithes and Chelmo.

In the same *Proceedings*, Mr. B. A. Bean figures the rare eel *Ahlia egmontis* from Barbados. It has been received also from the Tortugas.

In the *Mark Anniversary Volume*, Dr. C. R. Eastman discusses again the character of the extraordinary structures found in Carboniferous rocks and known as Edestus, with a bibliography of the subject. These are now believed to be coalescent whorls of teeth of some cestraciont shark.

In the *Proceedings of the Washington Academy of Sciences* (Vol. V, pp. 189–229), Messrs. Edmund Heller and Robert E. Snodgrass give an account of the new species of fishes taken in their expedition to the Galapagos under the auspices of the Hopkins Seaside Laboratory of Stanford University. The following are the new genera and species:

Evolantia for *Exœoctus micropterus*, *Sphyræna idiastes*, *Apogon atrodorsatus*, *Galeagra pammelas* (a new genus allied to Acropoma), *Corvula eurymesops*, *Sciæna perissa*, *Azurina eupalama*, *Pomacentrus redemptus*, *Pomacentrus arcifrons*, *Nexilosus albemarleus* (a new genus allied to Hypsypops), *Scarus noyesi*, *Pontinus strigatus*, *Eleotris tubularis*, *Cotylopus cocoënsis*, *Gobius rhizophoræ* (a species of Coryphopterus), *Gobius gilberti* (a species certainly referable to the Japanese genus Pterogobius), *Arbaciosa truncata*, *Malacoctenus zonogaster*, *Lepisoma jenkinsi*, *Encheliophis jordani*, *Petrotyx hopkinsi*, *Eutyx diagrammus* (Petrotyx and Eutyx are new genera of Brotulidæ), *Antennarius togus*, *Allector cheloniæ* (Allector is a new genus allied to *Chaunax*). A list of all the species constituting this splendid collection will appear later.

In the *Proceedings of the Biological Society of Washington* (XVI, 1903), Austin H. Clark shows that the earliest name of the common American Eel is *Anguilla chrisypa* Rafinesque, the name meaning "besmeared or anointed below." Rafinesque calls it "Gold-breast."

In the *Bulletin du Museum d' Histoire Naturelle* Paris (1903), Dr. Pellegrin describes a number of new species of Cichlidæ, one of them, *Heros* (*Cichlasoma*) *labridens*, being from Huasteca Potosina, from the veteran naturalist, Dr. Alfredo Dugès of Guanajuato. It is near *Cichlasoma bartoni*. Several others are from Guiana.

In the *Bulletin of the U. S. Fish Commission* (1902) Professor W. J. Mœnkhaus describes a new species of Darter, *Hadropterus evermanni* from Lake Tippecanoe in Indiana.

D. S. J.

BOTANY.

Notes.— Professor Ganong's address on the cardinal principles of ecology is published in *Science* of March 25.

Daniel gives an account of a graft-hybrid between pear and quince in the *Revue Générale de Botanique* of Jan. 15.

An account of DeVries' mutation theory, with portrait, is published by Harris in *The Open Court* for April.

The vegetative vigor of hybrids and mutations is considered by Cook in a leaflet of *Proceedings of the Biological Society of Washington*, issued April 9.

Nelson describes a number of new flowering plants from Nevada, and proposes new names for ten old species known under preoccupied names, in leaflets of *Proceedings of the Biological Society of Washington*, issued on April 9.

Pammel publishes an account of some weeds of Iowa as *Bulletin 70* of the Experiment Station of that State.

Miss Perkins has issued (Gebrüder Borntræger, Leipzig, January, 1904) the first fascicle of "Fragmenta Floræ Philippinæ," embodying the results of studies carried on at the Berlin Museum and based on the collections of Warburg, Merrill, Ahern and others.

Merrill has published, from the Manila Bureau of Government Laboratories, papers on new or noteworthy Philippine plants and the American element in the Philippine flora.

A list of the plants known from Siam, by Williams, is being published in current numbers of the *Bulletin de l'Herbier Boissier.*

Vol. 4, Sect. 2, of the *Flora Capensis*, under the editorship of Thiselton-Dyer, runs from Hydrophyllaceæ into Scrophulariaceæ.

A number of views of the vegetation of Samoa accompany an article on that group of islands, by Kellogg, in *Out West* for April.

Vol. 3, fascicle 1, of Coste's "Flore descriptive et illustrée de la France" deals with Scrophulariaceæ and Labiatæ.

An analysis of the vegetation of Madeira, by Vahl, has been issued from the Gyldendalske Boghandel, of Copenhagen.

A posthumous paper by Weber, published by Roland-Gosselin in January from the *Bulletin de la Société Centrale d'Agriculture, etc., de Nice*, deals with the restored genus Cleistocactus.

Certain Arizona cacti are illustrated in *The Gardener's Chronicle* of March 19.

Country Life in America for April contains an illustrated article by Julia E. Rogers on Magnolias.

An account of Mexican tea (*Turnera aphrodisiaca*) is published by J. U. Lloyd in the *Pharmaceutical Review* for April.

A note on Rudbeckia, by Pihl, in *Svenska Trädgardsföreningens Tidskrift* of January, is illustrated by colored figures of several cultivated species.

A series of ten illustrations, showing the development of an elm shoot, by Richards, is published in *Country Life in America* for April.

A third signature of Professor Greene's "Leaflets" continues his study of Polygonaceæ.

Holm's "Studies in the Cyperaceæ — XXI," published in *The American Journal of Science* for April, deals with new or little known species of Carex.

Parish begins a preliminary synopsis of Southern California Cyperaceæ in the *Bulletin of the Southern California Academy of Sciences* for March.

Certain Canadian mosses are enumerated by Cufoni in No. 7–9 of the *Bullettino della Società Botanica Italiana* of 1903, which also contains a note by Baroni on the botanic garden of Mt. Ætna.

The necessity for reform in the nomenclature of fungi is discussed by Earle in *Science* for March 25.

Copeland has an article on Californian fungi in *Annales Mycologici* for January.

Rehm publishes diagnoses of a number of North American Ascomycetes in *Annales Mycologici* of January.

An account of two hundred Portuguese fungi has been distributed by Professor d'Almeida of Lisbon.

Klebahn's "Die wirtswechselnden Rostpilze" (Gebrüder Borntræger, Berlin, 1904) forms a large volume containing a detailed analysis of heteroicism followed by an account of the species showing this peculiarity and ample indexes to fungi and hosts.

Taphria cœrulescens is the subject of *Bulletin 126* of the Alabama Experiment Station, by Wilcox.

Salmon gives an account of recent researches on the specialization of parasitism in Erysiphaceæ in *Annales Mycologici* for January, and *The New Phytologist* of Feb. 27.

An account of dry rot of the potato, caused by *Fusarium oxyspo-*

rum, by Smith and Swingle, is published as *Bulletin 55* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

Fungous diseases form the subject of *Bulletin 63* of the Delaware College Experiment Station, by Chester and Smith.

Oudemans has distributed separates from the Proceedings of Jan. 30 of the *K. Akademie van Wetenschappen te Amsterdam*, describing *Exosporina Laricis*, a new destructive parasite of the larch.

Arthur describes and figures the three common edible species of Coprinus in *Bulletin 98* of the Purdue University Experiment Station.

A paper by Stahl on the means by which lichens are protected against feeding animals is separately distributed from the *Festschrift* commemorative of Hæckel's 70th birthday, issued by the Fischer press of Jena.

The development of lichen apothecia is considered by Baur in the *Botanische Zeitung*, Abteilung I, of March 1.

Coville has recently distributed separates of a well illustrated paper on the Indian use of *Nymphæa polysepala*, from the *Report of the U. S. National Museum* for 1902.

An account of a new African fiber-banana, *Musa ulugurensis*, is given by Warburg and Moritz in *Der Tropenpflanzer* for March.

Van Es and Waldron give an account of stock-poisoning plants of North Dakota in *Bulletin 58* of the Experiment Station of that State.

An illustrated account of lumbering by machinery is contributed by K. Smith to *The World's Work* of February.

Clement is publishing a series of illustrated articles on "the Japanese floral calendar" in current numbers of *The Open Court*.

The reports on the New York Botanical Garden for 1903, contained in Vol. 3, No. 10, of the *Bulletin* of the institution, show that 84,163 specimens were added to the herbarium, 1,656 bound volumes were added to the library, and 1,000 species were added to the living collection, bringing the latter up to about 11,600 species.

An illustrated account of the Arnold Arboretum, by Miller, is published in *Country Life in America* for March.

40,396 visitors to the conservatories of the St. Petersburg Botanical Garden, in 1903, are reported in its *Bulletin* of March 5.

A portrait of Behrens is published as frontispiece to Heft 79 of the *Zeitschrift für wissenschaftliche Mikroskopie*.

PUBLICATIONS RECEIVED.

(Regular exchanges are not included.)

ANNANDALE, N. and ROBINSON, H. C. Fasciculi Malayenses Anthropological and Zoölogical Results of an Expedition to Perak and the Siamese Maylay States. 1901–1902. Pt. I, Zoölogy, pp. 1–200, pls. 1–10; Pt. II, Zoölogy, pp. 201–307, pls. 11–14–vii; Supplement pp. xlii and map.— BAILEY, L. H. Plant Breeding. Being five Lectures upon the Amelioration of Domestic Plants. Third Edition, New York, Macmillan, 1904. 8vo, xiii + 324 pp., 22 figs.— BASTIAN, H. C. Studies in Heterogenesis. London and Oxford, Williams and Nargate, 1903. 8vo, viii + 354 + xxxiii, pp., 815 figs. 31/6.— BERGEN, J. Y. Notebook to Accompany Bergen's Text Books of Botany or for general use in Botanical Laboratories of Secondary Schools. Boston, Ginn & Co., 1904. 4to, 144 pp., $0.75.— DAVISON, A. Mammalian Anatomy with Special reference to the Cat. Philadelphia, Blakiston, 1903. 8vo, xi + 250 pp., 108 figs. $1.50.— GARDINER, J. S. The Fauna and Geography of the Maldive and Laccadive Archipelagoes, etc. Vol. II, Part III, pp. 589–698, pls. 35–48.— GIRARD, A. Controverses Transformistes. Paris, C. Naud, 1904. 8vo, 178 pp., 23 figs.— LEIGHTON, G. R. The Life-History of British Lizards and their Local Distribution in the British Isles. Edinburgh, Geo. A. Morton, 1903. 8vo, xiv + 214 pp., many illustrations.— MOUILLEFERT, P. Traité de Sylviculture. Exploitation et Aménagement des Bois. Paris, Alcan. 1904. 8vo, 476 pp., 10 pls., 27 figs. 6 francs.— MOUNEYRAT, A. La Purine et ses Dérivés. "Scientia," Serie Biologique, No. 18. Paris, C. Naud, 1904 8vo. 98 pp.— NILES, GRACE G. Bog-trotting for Orchids. New York, Putnam's. 1904. 8vo, xvi + 310 pp., 72 plates, 24 of them colored.— PERRY, J. H. and EMERSON, B. K. The Geology of Worcester, Massachusetts. Worcester Natural Hist. Soc., 1903. 8vo, xii–166 pp., plates and maps.— PORTER, T. C. Flora of Pennsylvania. Boston, Ginn & Co., 1904. 8vo, xv + 362 pp. $2.00.— PORTER, T. C. Catalogue of the Bryophyta (Hepatics, Anthocerotes and Mosses) and Pteridophyta (Ferns and Fern-allies) found in Pennsylvania. Boston, Ginn & Co., 1904. 8vo, 66 pp.— REESE, A. M. An Introduction to Vertebrate Embryology Based on the Study of the Frog and the Chick. New York, Putnam's, 1904. 8vo, xvii + 291 pp., 83 figs.— SCRIBNER, G. H. Where did Life Begin? A Brief Inquiry as to the Probable courses of Migration therefrom of the Flora and Fauna of the Earth. A Monograph. New York, Scribner's, 1903. 8vo, xiii + 75 pp., portrait. $1.20.— SNYDER, H. The Chemistry of Plant and Animal Life. New York, Macmillan, 1903. 8vo, xvii + 406 pp., 102 figs. $1.40.—STEINMANN, Z. Einführung in die Paläontologie. Leipzig. Engelmann, 1903. 8vo. ix + 466 pp., 818 figs. 12 marks.— TAYLOR, J. W. Plane Geometry. Boston, Ginn & Co., 1904. 8vo, viii + 171 pp., 58 figs.

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THE AMERICAN NATURALIST

A MONTHLY JOURNAL
DEVOTED TO THE NATURAL SCIENCES
IN THEIR WIDEST SENSE

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THE AMERICAN NATURALIST is an illustrated monthly magazine of Natural History, and will aim to present to its readers the leading facts and discoveries in Anthropology, General Biology, Zoology, Botany, Paleontology, Geology and Physical Geography, and Mineralogy and Petrography. The contents each month will consist of leading original articles containing accounts and discussions of new discoveries, reports of scientific expeditions, biographical notices of distinguished naturalists, or critical summaries of progress in some line; and in addition to these there will be briefer articles on various points of interest, editorial comments on scientific questions of the day, critical reviews of recent literature, and a quarterly record of gifts, appointments, retirements, and deaths.

All naturalists who have anything interesting to say are invited to send in their contributions, but the editors will endeavor to select for publication only that which is of truly scientific value and at the same time written so as to be intelligible, instructive, and interesting to the general scientific reader.

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THE

AMERICAN NATURALIST.

VOL. XXXVIII. *July–August, 1904.* NOS. 451–452.

PROCEEDINGS OF THE AMERICAN SOCIETY OF ZOÖLOGISTS.

FIRST ANNUAL MEETING OF THE EASTERN BRANCH.

THE first annual meeting of the Eastern Branch of the American Society of Zoölogists, the fourteenth annual meeting of the Society since its establishment as the American Morphological Society, was held in Biological Hall, University of Pennsylvania, Philadelphia, Pa., on Tuesday and Wednesday, December 29 and 30, 1903.

In accordance with the report of the committee appointed at the preceding meeting to consider the matter of the publication of the proceedings of the Society, of an official organ, etc., it was voted to be the sense of the Eastern Branch of the American Society of Zoölogists that the *American Naturalist* should become the official organ of the Society, and the committee was empowered to arrange for the publication of this year's proceedings of the Eastern Branch in the *American Naturalist*.

The committee in charge of the preparation of an invitation to the International Zoölogical Congress to hold its meeting in 1907 in America, presented its report, which was adopted. As the result of this action, and similar action by the Central

Branch, the American Society of Zoölogists will invite the International Zoölogical Congress to meet in America in 1907. The necessary preliminary arrangements have been left to a committee. The committee appointed to draw up a definition of zoölogical requirements for admission to college, conformable with the definition of the requirements in other sciences, published by the College Entrance Examination Board, submitted a report of progress that caused considerable discussion, and the committee was continued.

The list of officers for 1904 is as follows:

President, E. A. Andrews; vice-president, W. E. Castle; secretary-treasurer, G. A. Drew. Additional members of the executive committee, T. H. Montgomery, Jr., H. C. Bumpus, H. S. Jennings.

The following are abstracts of papers presented at the meeting:

The Egg Cases of Chimæroid Fishes: Bashford Dean, Columbia University. — The egg cases of chimæroid fishes present an extreme case of adaptation, not to the egg of the time it is placed in the capsule, but to the young fish when about to escape. From this standpoint the capsule is adapted in the matter of extreme size, definite modeling to the head, trunk and tail of the young fish, durability, mode of attachment, position, which enables the young fish to develop dorsal side upward, orientation, wherein the snout of the young fish develops in the direction of the opening valve, and the tail in the direction of the long and narrow end of the capsule. Further adaptations include an elaborate provision for circulation of water within the capsule, the mechanism for which improves as the embryo develops, by means of a process of weathering, whereby the perforations of the capsule become progressively larger; and a special exit valve which can be opened only from within, and only at the time when the fish is ready to escape. The exit valve has then a kind of tension resulting in "dehiscence," comparable somewhat to that of the elements of a seed pod. Adaptation is made still more complete by provision for the specific characters of the adult; thus the species which have the longest tails have the

longest tail sheaths in the egg capsules, and those having the deepest bodies have also the deepest cavity in the main portion of the capsule.

The foregoing characters evidently cannot be explained by the Lamarckian hypothesis, for so perfect a case could not have been formed primitively *in utero* around the embryo; for, by the principle of use and disuse itself, such an elaborate capsule would not have been formed for the protection of an embryo which was just about to be hatched, nor would the capsule be provided for aquatic breathing. It is, moreover, a well known law that in uterine development the secondary membranes are reduced rather than increased. Natural selection, as it is generally understood, is equally inadequate to explain the formation of the present capsule; for, from this standpoint, fluctuating variations would have had to be selected throughout a long series of complicated changes in two entirely different lines, *i. e.*, in the line of the evolution of the embryo and in that of the evolution of the capsule. And it is more than difficult to imagine that in each of these parallel series the corresponding favorable fluctuations could have continued to be successively selected. This series of constantly adapted stages furnishes a notable example of development in a definite line.

The Reproductive Organs of the Limbless Lizard Anniella: W. R. Coe and B. W. Kunkel, Yale University.—The subject of this investigation, *Anniella pulchra*, lives on the barren sand plains in certain portions of California and Arizona. It is a slender, worm-like lizard, entirely devoid of limbs and limb girdles except for slight rudiments of the pelvic arch. It lives beneath the surface of the sand and feeds upon small insects and spiders.

Although described in 1852, it has never been carefully studied except with regard to its external anatomy and skeleton.

An examination of its viscera reveals a number of interesting anatomical peculiarities, among which those of the reproductive organs are perhaps the most striking. These relate particularly to the oviducts and uterus of the female and the copulatory organs of the male.

As in many other lizards, Anniella is ovoviviparous. The young, only two of which are produced in a season, are born in

September. Both of these develop in the right oviduct (Fig. 1, *ut*, *ut'*), the left being very rudimentary and apparently quite functionless (Fig. 1, *l. od*). The right and left ovaries are equally well developed and a single ovum matures in each, but both ova enter the right oviduct.

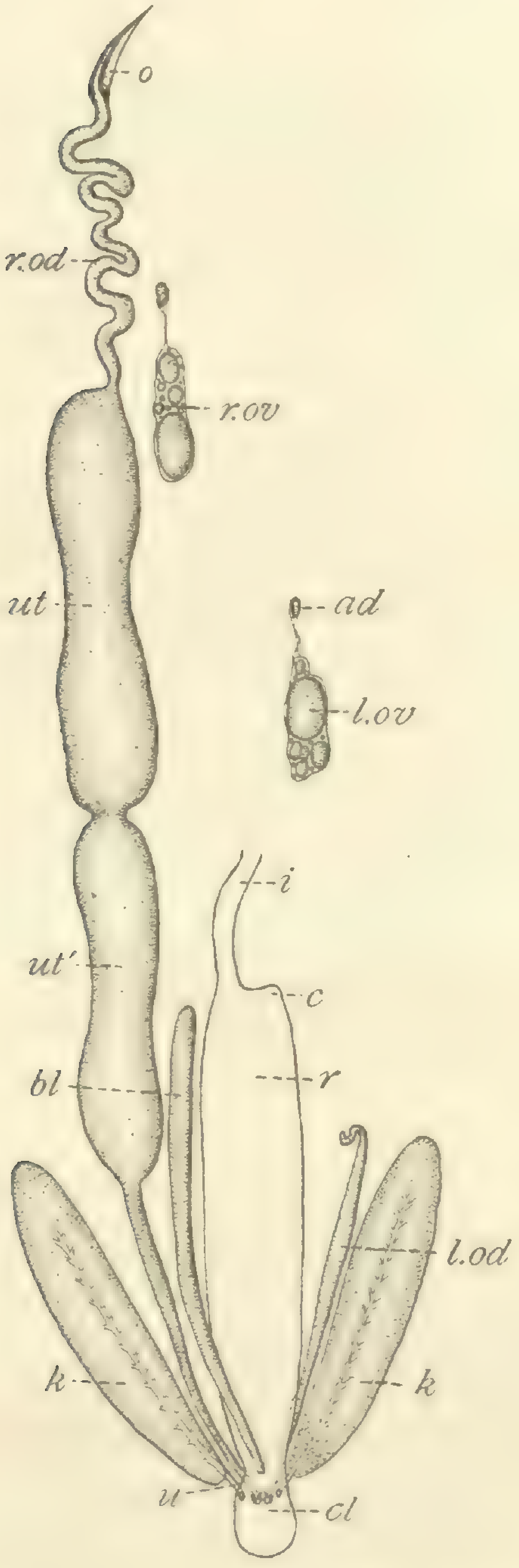


Fig. 1.— Diagram of the urogenital organs of Anniella, showing the right oviduct (*r. od*) with the two developing embryos (*ut*, *ut'*) in the uterus, the rudimentary left oviduct (*l. od*), and the ovaries (*l. ov* and *r. ov*); *ad*, adrenal body; *o*, ostium of right oviduct; *bl*, urinary bladder; *k*, **kidney**; *u*, **ureter**; *cl*, cloaca; *i*, ileum; *c*, rudimentary cæcum; *r*, rectum. × 3.

The rudimentary left oviduct is represented by a slender tube usually extending forward only about as far as the anterior ends of the kidneys, which are situated in the most posterior portion of the body cavity (Fig. 1, *l. od*). The anterior end of this aborted oviduct is terminated by a very narrow canal which usually shows a tendency to become more or less convoluted. It is especially noteworthy that this convoluted, terminal canal shows great variation in length in different individuals. In a single specimen examined it was about half as long as that of the functional right oviduct. In this single instance the rudimentary oviduct is terminated anteriorly by an ostium opening into the body cavity. The posterior end of the left oviduct is but little smaller than that of the right, and has a similar structure and similar relations with the cloaca.

These peculiarities furnish a striking example of what appears to be a very recently acquired anatomical character — one which

has not reached a condition of stable equilibrium, as instanced by the great variation of the parts concerned. The left oviduct has apparently been eliminated as a functional organ of the body, and yet the case mentioned where it was half as long as the functional one suggests the possibility of further variations, which, in an exceptional case, might show a reversion to the primitive condition in which an embryo might develop in this now rudimentary organ.

So far as we are aware no instance of an aborted and functionless oviduct has been reported for any of the lizards. The related genus, Anguis, of Europe, has both oviducts well developed. In many reptiles, however, the left is shorter than the right oviduct, so that Anniella presents a variation along the same line as these other reptiles, but one which has been carried to an extreme condition.

It should be pointed out that it is the left oviduct which is aborted in Anniella, while it is the right which has become functionless in birds. In the latter, however, the degeneration of the parts is carried to a greater length in that the right ovary is

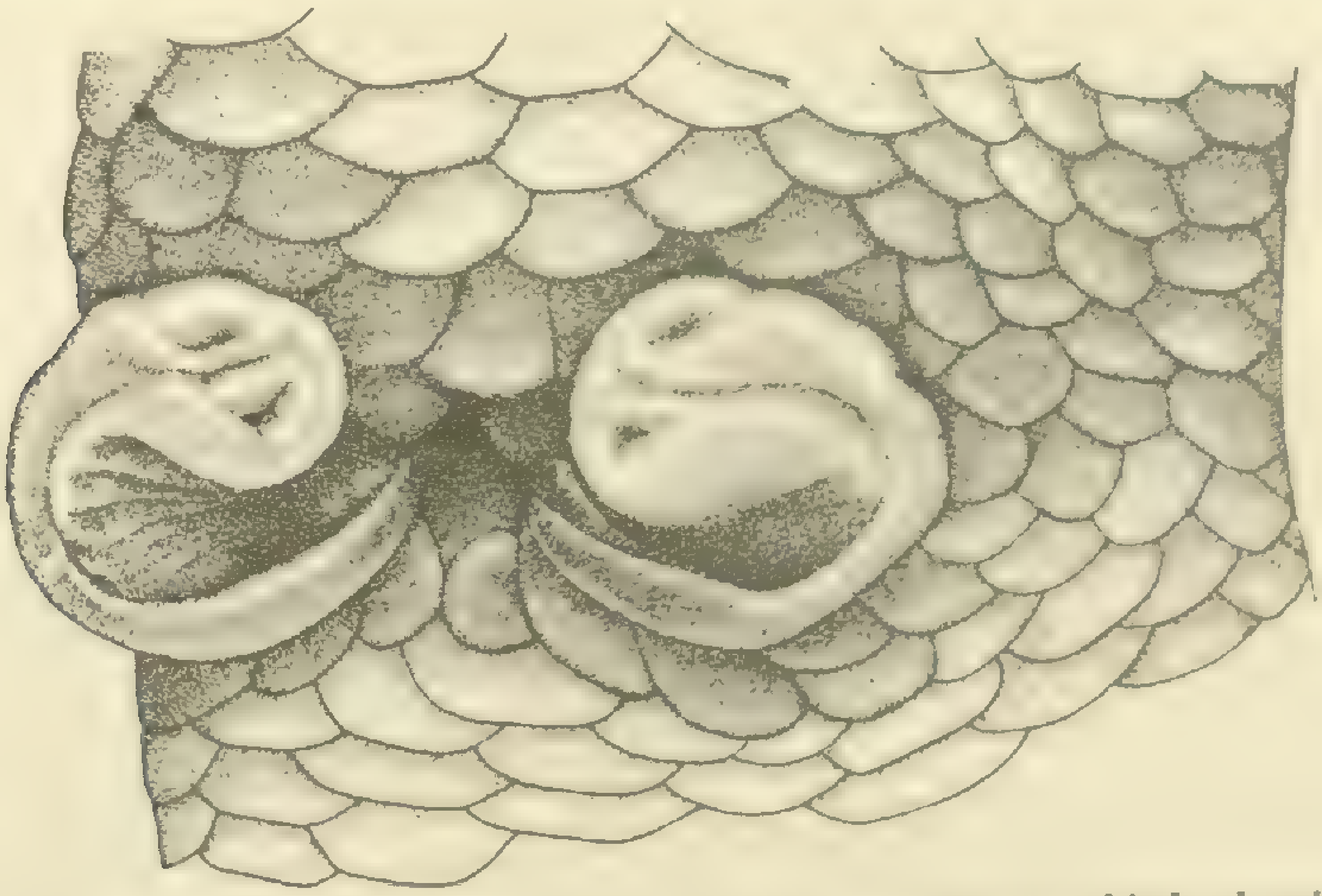


Fig. 2.— Portion of ventral surface of embryo of Anniella shortly before birth, showing the pair of large copulatory organs (phalli) projecting from the lateral borders of the cloacal aperture and the oblique groove and terminal pits with which each phallus is provided. × 22.

likewise more or less aborted, while in Anniella both ovaries retain their normal functions.

In the male the spermaries and the sperm ducts are developed equally on the two sides of the body. The copulatory organs (phalli) are formed as finger-like, external projections from the

lateral borders of the cloacal aperture, and nearly to the time of birth have a curious resemblance to a pair of rudimentary limbs (Fig. 2). Shortly before birth they are drawn into the cloacal aperture, and by a process of invagination are converted into a pair of slender pouches which extend backward into the caudal region for a considerable distance behind the cloaca. They then lie on the ventral side of the tail and immediately internal to the muscles of the integument.

It is a remarkable fact that these copulatory organs develop in females as well as in males. In females, however, they cease their development after they are converted into post-cloacal pouches, although they are retained throughout the life of the animal. In the males, on the other hand, they increase greatly in size at the time of sexual maturity. During the act of copulation the large blood sinuses with which they are provided become distended with blood. This surcharging with blood, together with the contraction of certain muscles which surround the pouches, causes the phalli to be everted to their original, embryonic condition, and thus to function as a pair of true copulatory appendages.

Some Account of the Temporary Biological Station at Bermuda for the Season of 1903: Charles L. Bristol, New York University.— The following invitation was issued about May 1, 1903:

Harvard University and New York University unite with the Bermuda Natural History Society in inviting botanists and zoölogists to spend six weeks in the temporary biological station provided for the present season at Bermuda.

By special arrangements with the Quebec S. S. Co. and the Hotel Frascati it has been possible to make the total expense, including transportation from New York and return, and board and lodging for six weeks at Bermuda, one hundred dollars.

The Bermuda Natural History Society has expressed its intention to do everything in its power to make the summer's work as profitable and pleasurable as possible, and to this end has undertaken to provide, among other things, the necessary facilities for collecting, namely, a steam launch, thirty to forty feet long, with crew; a sail boat with fish-well and crew; three rowing

boats, and a carriage with two horses, capable of carrying ten or twelve persons. The laboratory will be equipped with all necessary reagents and utensils except microscopes and dissecting instruments, which should be brought by each investigator.

The well known richness of the sub-tropical fauna and flora, the healthfulness and equable temperature of the islands, and the ease with which they may be reached combine to make the Bermudas a most attractive field for biological research.

Venerable George Tucker, Archdeacon, President Bermuda Natural History Society.

Hon. W. Maxwell Green, Consul U. S. A., Vice-president B. N. H. S.

F. Goodwin Gosling, Honorary Secretary B. N. H. S.

E. L. Mark, Director of Zoölogical Laboratory, Harvard University.

C. L. Bristol, Professor of Biology, New York University.

It met with a hearty reception, and in response to it thirty-three botanists and zoölogists from widely scattered portions of the United States availed themselves of the opportunity offered. The committee in charge was somewhat embarrassed at first, as our temporary laboratory was equipped for twenty research students, but the proprietor of the Hotel Frascati kindly gave up two large rooms in the hotel so that all were comfortably cared for.

The facilities provided and paid for by the Bermuda Natural History Society enabled the party to make daily excursions either by launch to the reefs and lagoons, by wagons to botanical collecting localities, or by rowboat to the nearby places.

During the season Capt. W. E. Myers of St. George placed his powerful sea-going tug, "Gladisfen," at the disposal of the expedition to collect on the "Challenger" bank. The trip occupied three days and was very fruitful in results.

During the stay of the party, between June 22 and August 22, the weather was pleasant save one or two days of dead calm, when it was disagreeably warm, though at no time did the thermometer go above 85° F. The general health of the party was excellent, and demonstrates what my experience had led me to believe, — that the climate is favorable for college workers in midsummer.

The accommodations at Hotel Frascati were excellent. Our party so nearly filled the house that the proprietor, Mr. Alonzo Peniston, put it practically at our disposal, accommodating his meals to our excursions whenever it was desired. The table was first-class, and not to be compared with the usual summer board at seaside laboratories. The food was well cooked, was abundant, and well served at tables always decked with a profusion of flowers.

The party was welcomed on its arrival at the dock by the venerable Archdeacon Tucker, Hon. W. Maxwell Greene and Mr. F. Goodwin Gosling, and this welcome was continued by every one — high and low — during the season. His Excellency, the Governor, Gen. H. LeG. Geary, was kind enough to extend a hearty welcome to the party by holding a reception at Mt. Langton, to which nearly two hundred guests were invited. Hospitality was extended on all sides, and almost to the embarrassment of the work at times.

The people of Bermuda became interested in the annual visits of the New York University Biological Expeditions from 1897 to 1902, and in 1902 a committee of the Legislature was appointed to consider and report on the advisability of the establishment of a Marine Biological Station. The Colonial Secretary, by direction of His Excellency the Governor, addressed a letter asking for information and coöperation to the following: the British Association for the Advancement of Science, the Carnegie Institution, the Royal Society, the Minister of Marine and Fisheries, Canada, Dr. Auton Dohrn, Naples. The responses were all heartily in favor of the idea, and this encouraged His Excellency to ask the approval of the Imperial Government. This was granted in a despatch from the then Secretary of State for the Colonies, Hon. Joseph Chamberlain, and the way was clear for further action by the Colony. In November, 1903, Governor Geary sent a message to the House of Assembly which has resulted in appropriate legislation without a dissenting voice.

It may be safely said now that before long a well equipped station will be available for biologists at Bermuda that will be open the year round.

During the coming summer another "temporary" station

will be established and good facilities offered for advanced workers.

A Key to the Development of Sipunculus nudus[1]: John H. Gerould, Dartmouth College. — The development of Phascolosoma shows that the embryonal envelope or serosa of *Sipunculus nudus*, described by Hatchek, is a modified prototroch. In the gastrula stage of each form the prototroch consists of two or three rows of broad, flat cells which encircle the embryo. In the trochophore of *Ph. vulgare* the apical plate, the mid-dorsal cord of ectoderm in the interruption of the prototroch and the somatic plate are strikingly similar to the corresponding parts in *S. nudus*, but in the former no sinking beneath the vitelline membrane occurs, and no amniotic cavities are formed. The resemblance between the trochophores extends even to the apical rosette and to the cells which bear the postoral circlet of cilia.

The remnants of the prototroch of Sipunculus are cast off with the vitelline membrane, the huge prototroch cells of Phascolosoma degenerate during metamorphosis, and their substance in the form of yolk granules passes backward into the newly formed cœlom. Thus the cœlom of the larva becomes filled with yolk granules, which Selenka mistook for blood corpuscles. These gradually are absorbed. A cuticula is formed beneath the vitelline membrane, the latter is shed, and an overgrowth of the region vacated by the prototroch cells takes place.

Sipunculids are primitive Trochozoa, closely allied to chætopods. The adult sipunculid retains the retractor muscles and nephridia of the trochophore; and the loss of the prototroch, development of the cœlom and elongation of the trunk are the only fundamental changes which the trochophore undergoes in passing into the adult form. Resemblance of the trochophore of Phascolosoma to that of chætopods, *e. g.*, Amphitrite, is striking. Transitory metamerism of the mesoblastic bands and

[1] The reader is referred, for a more complete account, to Studies on the Embryology of the Sipunculidæ. I. The Embryonal Envelope and its Homologue. *Mark Anniversary Volume.* Cambridge, Mass., 1903; and The Development of Phascolosoma (preliminary note). *Archives de Zoöl. expér. et gén. Notes et Revue.* 4e série, T. 2, No. 2, 1904. p. xvii–xxix.

of the fundament of the nerve cord in *Ph. gouldii*, immediately before metamorphosis, points definitely to an intimate relationship between the sipunculids and the annelids. Sipunculus is more highly modified than Phascolosoma.

Divergence Under the Same Environment as Seen in the Hawaiian Snails: John T. Gulick, Oberlin, Ohio.— The Island of Oahu presents two mountain ranges; one near the northeast coast, about 35 miles in length, and enjoying a heavy rainfall, especially on the side of the range most exposed to the northeast trade-winds; the other, near the southwest coast, about half as long, and receiving much less rain. The forest regions on these two mountain ranges are occupied by about 300 species of snails belonging to eight genera of the family Achatinellidæ. A large majority of these species belong to four genera found always on the trees or other vegetation. Auriculella clings to the leaves, is about the size of a grain of wheat, and is represented by one abundant species on the dry mountain range, and by several species on the other range. Apex is from half an inch to an inch in length, and occupies the dry range, and the drier ridges of the other range. Achatinella and Bulimella are in size not very different from Apex, and like it are found on the trunks and branches as well as on the leaves; but their distribution is almost entirely on the longer mountain range, Achatinella being more abundant on the less rainy side, and Bulimella prevailing on the more rainy side.

Natural selection has undoubtedly been an important factor in adapting Bulimella for the rainiest districts; and Achatinella and Bulimella for the shady groves of the less rainy region, and Apex for the driest region as well as for the deficient shade on the ridges of the intermediate region.

But we come now to species whose divergence refuses to be explained by either natural selection or sexual selection. As an example of divergent evolution that must depend on other controlling principles, let us consider the formation of the series of species of Achatinella occupying the valleys on the southwest side of the main mountain range. The temperature, the rainfall, the soil, and the plant and animal species surrounding these snails are much the same.

Commencing at the most eastern of these valleys and proceeding toward the northwest, we find that the first seven or eight miles brings us past about that number of deep valleys, occupied by shady groves and inhabited by many varieties belonging to fifteen or more species. These species are all of the larger type of the genus, being near an inch in length. With some of them, all the individuals of the species are found in the groves of a single valley, and in the case of most, even stragglers are not found at a distance of more than a mile from the metropolis of the species.

Proceeding toward the northwest, we find that the genus is represented by many species, of progressively diminishing size, till at the other end of the mountain range the shells have dimensions not more than half those presented by the shells found in the valleys first explored. The habits of feeding are also wholly different; for as we approach the northwest end of the range we find that the larger trees have been deserted, and the shrubs and herbs have become the homes of most of the species. This diversity either in the inherited aptitudes or in the acquired habits of the isolated groups of one stock, resulting in different methods of dealing with the same environment, undoubtedly results in different forms of selection helping to mould the different groups into different species. We, however, note that, in these cases, the process is not natural selection: for it is not difference in the environment causing the accumulation of divergent adaptations, but it is slightly divergent adaptations, protected by isolation from the swamping effects of free-crossing with the original stock, that initiates divergent methods of dealing with the same environment, and so determines the difference in the selection which emphasizes the divergence. This form of selection, determined by the aptitudes and habitudes of the species in dealing with the environment, I call endonomic selection.

A point of very great interest is the important part filled by isolation in producing divergent forms of endonomic selection. If a pair of individuals from a plastic (or variable) species are completely isolated from the original stock, the probability is that in some way their method of dealing with the environment

will differ from the method prevailing in the original home, though under certain circumstances it may have been tried by some of the original stock. New relations having been established with the environment, and the swamping effect of association and intergeneration being removed, divergent evolution is insured. Two genera of the Achatinellidæ are found almost exclusively on the ground among the dead leaves. The divergence between these genera living on the ground and those living on the trees and shrubs was probably gradually introduced in some such way. In the same way may have arisen the differences between the genus of minute species feeding on the leaves and the genera of larger forms feeding on what is found on the trunks and branches of the trees.

The Function of the Lateral Line Organs in Fishes: G. H. Parker, Harvard University. — This work was carried on at the Biological Laboratory of the United States Bureau of Fisheries at Woods Hole, Massachusetts. Tests were made on smooth dogfish, skates, winter flounders, scup, and two species of Fundulus. The action of the lateral line organs was eliminated by cutting the branches of the fifth, seventh, and tenth nerves supplied to these organs. After recovery from shock the reactions of individuals on which these operations had been carried out were compared with those of normal fishes. No significant differences could be discovered in the reactions of normal and operated fishes to the following stimuli: temperature changes from 9° C. to 30° C.; salinity changes having a range between a mixture of one part sea water and four parts fresh water, and sea water concentrated to three fourths its original volume; reduced oxygen supply; increased carbon dioxide; foul water; reduction of pressure to nine pounds; increase of pressure to twenty-two pounds; and currents of water. On testing for equilibrium it was found that the lateral line organs were of no more significance in this respect than the general integument. Normal and operated fishes did not respond differently to sound vibration of the rate of 100 per second. Operated fishes failed to respond to vibrations at the rate of six per second, whereas normal fishes reacted to these with great precision. The lateral line

organs are, therefore, concerned with vibrations of low frequency. These vibrations are often produced when large objects move in the water or when wind blows on its surface.

The Sexual Elements of the Giant Salamander: Albert M. Reese, Syracuse University. — Eggs and spermatozoa were obtained by stripping giant salamanders (*Cryptobranchus alleghaniensis*) during the latter part of September.

Each egg is a spherical mass of yellow yolk, about 6 mm. in diameter, surrounded by two layers of transparent jelly; it does not completely fill the inner envelope, but is surrounded by an aqueous fluid.

The egg proper is filled with yolk granules of various sizes, and is surrounded by a thin vitelline membrane.

The gelatinous envelopes are continued as slender cords from egg to egg, forming a continuous string similar to the egg-strings of Amphiuma. The distance between two adjacent eggs is about four or five times the diameter of a single egg.

Some dozens of eggs were obtained from one female, all of them apparently being derived from one ovary.

The spermatozoa, in which no motion could be seen, though stripped with little difficulty from the males, consist of an elongated, cylindrical nucleus, a sharp, gradually-tapering apical body, and a tail of moderate length which consists of a central fibre and a transparent envelope. No middle-piece can be made out.

Artificial fertilization was attempted but was entirely unsuccessful.

Some Recently Discovered Cases of Mutual Sexual Adaptation: P. P. Calvert, University of Pennsylvania. — In studying the Odonata of Mexico and Central America for the *Biologia Centrali-Americana* it was found that a new species of Protoneura, *P. peramans*, presented a remarkable adaptation of the sexes for mutual grasping during pairing, in that the bifid, superior, terminal, abdominal appendages of the male are received between bifid, mesothoracic processes of the female. The other species of this genus from this region show no (or less perfect) adaptations in this regard.

Segmentation of the Ovum of Desmognathus fusca:[1] William A. Hilton, Cornell University. — During the last few years several amphibian eggs have been found which, from the few stages of development described, seem to indicate a meroblastic rather than a holoblastic method of cleavage. The first of these was reported by H. H. Wilder (1899) for Desmognathus, the second for Autodax, by Ritter and Miller, also 1899, and the third by Montgomery for Plethodon in 1901. In all of these forms only the later stages were observed.

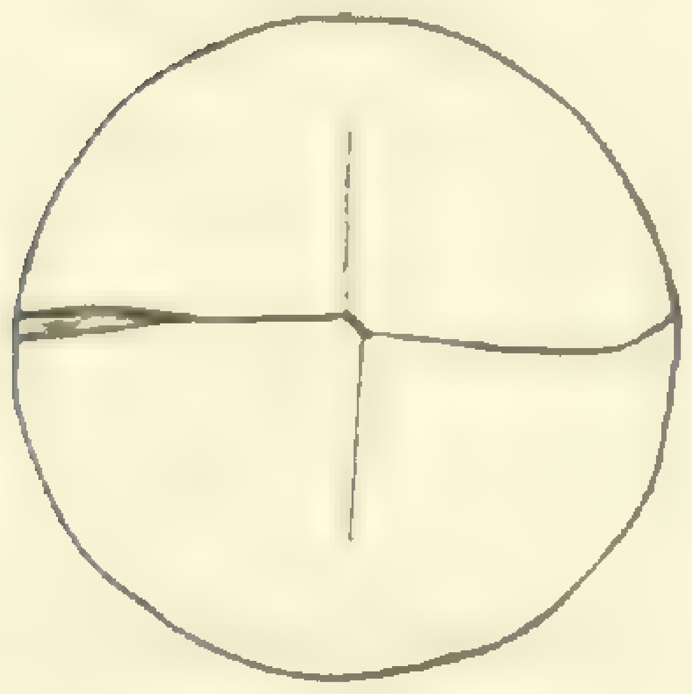


FIG. 1.— Surface view of a four-cell stage from above (about × 8).

As Desmognathus is very abundant in central New York, advantage was taken of the opportunity for a thorough investigation of the earlier stages.

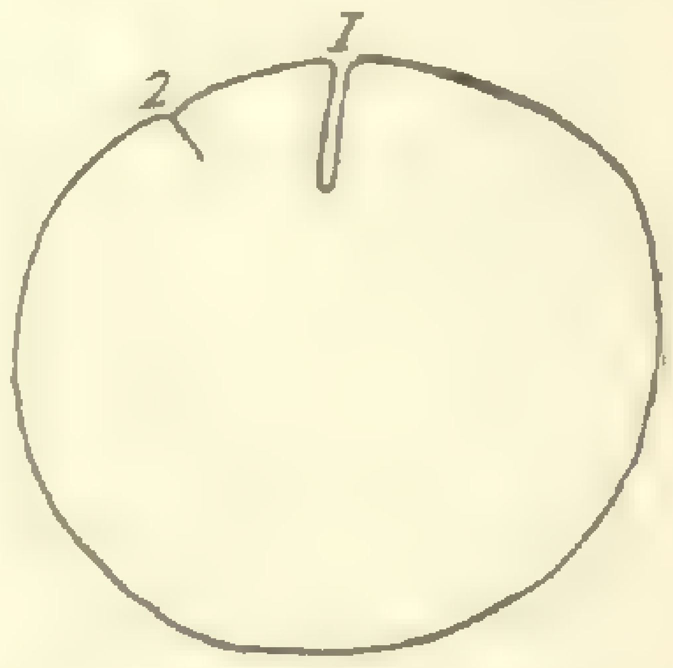


FIG. 2 — Section of four-cell stage, 1 and 2, first and second division planes (about × 8).

The eggs are about 3.5 mm. in diameter and entirely devoid of pigment. The general appearance is creamy white except at the animal pole, which is chalky white. In this chalky white area the first division furrows make their appearance. The first and second furrows are at right angles (Fig. 1), but soon these lose this geometrical regularity and the later division lines may be very irregular.

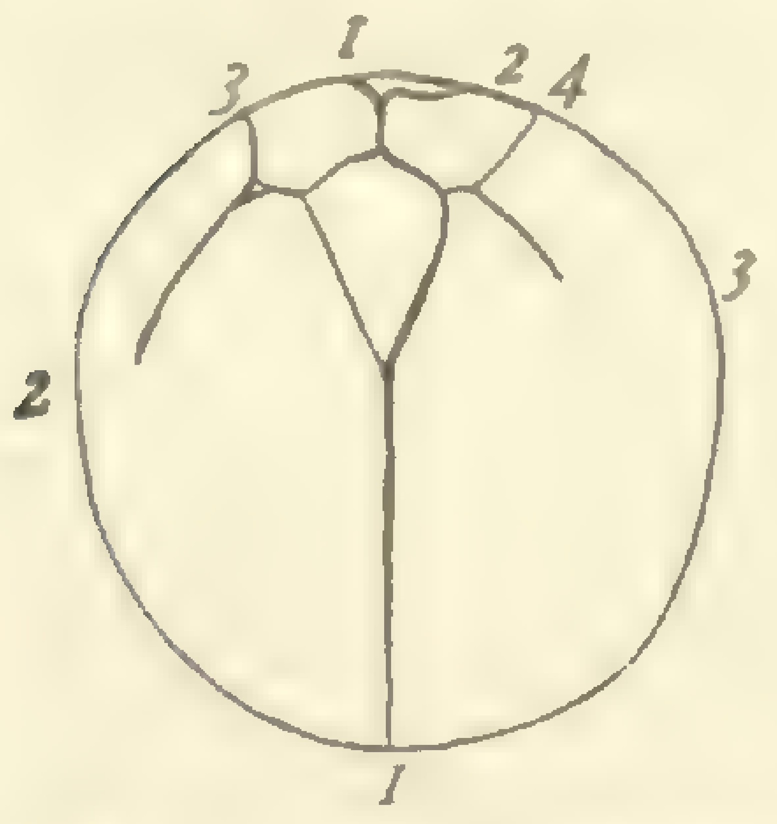


FIG. 3— Surface view of an eight-cell stage from the side, *1* and *2*, etc., first and second, etc., division planes (about × 8).

In the four-cell stage the first cleavage plane has cut somewhat deeper than the second, but neither has yet cut deeply into the central mass of yolk (Fig. 2). In the

[1] Due to a slight misunderstanding, both Dr. Wilder and the author have been working on precisely the same problem. Dr. Wilder's results, if not published by the time this appears, will be published soon. In his paper he comes to the conclusion that the eggs of Desmognathus are holoblastic and not meroblastic in cleavage. His conclusions were reached by the study of the surface views, and I am very glad of the opportunity to confirm his observations by the aid of a few sections of early stages as well as a few surface views. I will leave a more detailed account of the early development of this animal for a later paper.

next stage there is no distinct equatorial groove. The eight-cell stage is gradually derived from the four-cell condition by the appearance of furrows between the two original ones. In the eggs of this stage which Wilder has studied (see footnote) two rather regular vertical planes of cleavage cut the egg at nearly right angles to the first division plane, but in a considerable number of eggs which I have examined, some of them living and others preserved, I only found one or two with such regular vertical cleavage planes; in some there was an approach to it, but in a number of others the eight-cell condition seemed to be gradually derived from the four-cell stage by the appearance of furrows which were hard to recognize as parts of vertical planes of cleavage. In the eight-cell stage the first furrow nearly encircles the egg, but the position of the first and the second is often so shifted that it is difficult to believe that they were ever at right angles (Fig. 3). At this time the animal pole may be divided into one or more distinct blastomeres, but the vegetative pole shows almost no signs of cleavage planes (Fig. 4).

Fig. 4.— Section of an eight-cell stage (about × 8.)

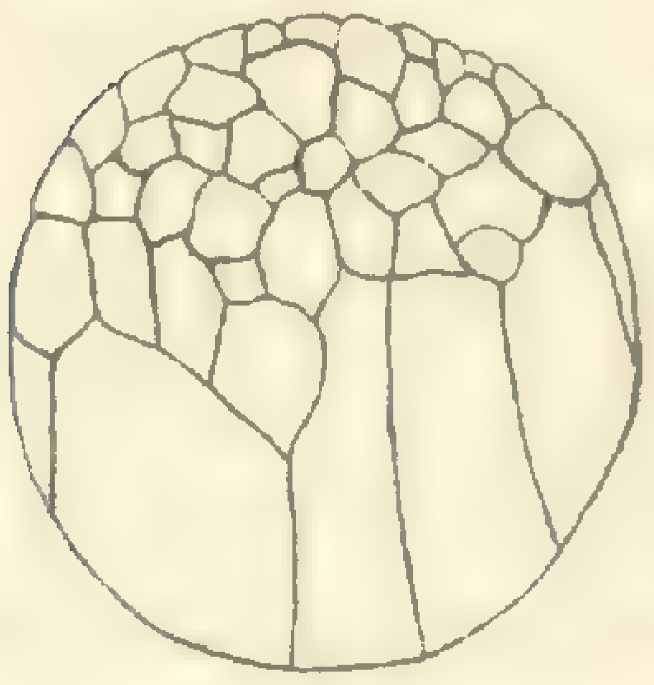


Fig. 5.— Surface views of a few-cell blastula from the side (about × 8).

As segmentation proceeds the surface appearances correspond in general with those of other amphibian ova (Fig. 5), but sections bring out the fact that the segmentation is shallow, and does not involve the whole thickness of the egg (Fig. 6). Later, however, when the surface appearance is like that of a fine celled blastula (Fig. 7), sections show that the segmentation has extended through the entire egg and that the cleavage in this stage is as truly holoblastic as in any other of the salamanders (Fig. 8).

Fig. 6.—Section of a few-cell blastula (about × 8).

As the embryo increases in size the cell outlines in the yolk are lost, and if sectioned in this stage only, one would be justified in suspecting a meroblastic segmentation. This

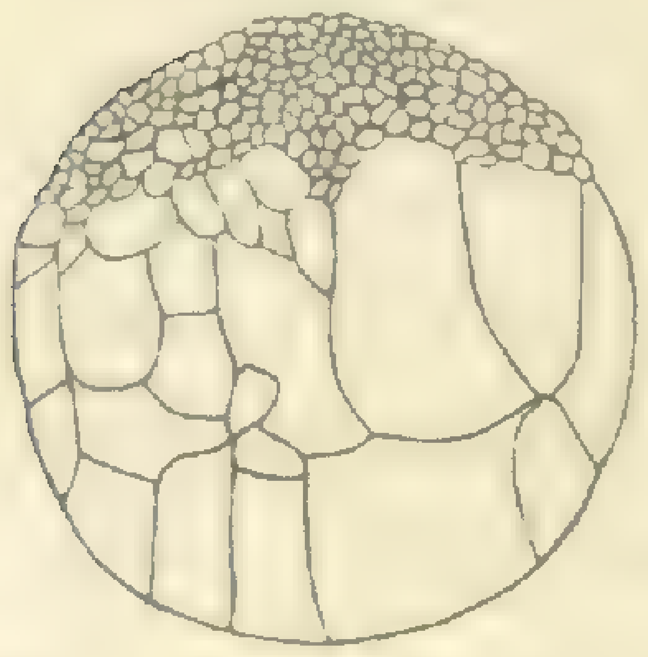


Fig. 7.— Surface view of a many-cell blastula from the side (about × 8.)

idea is helped by the fact that the growing embryo soon comes to occupy a position on the yolk strikingly like that of a fish embryo.

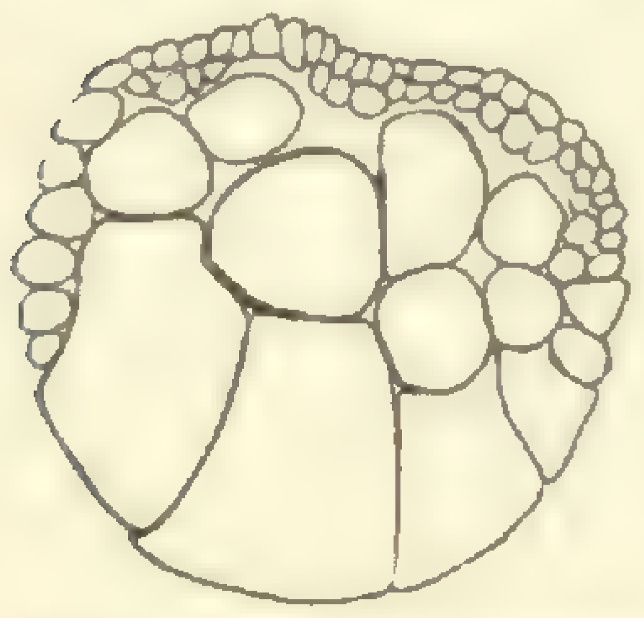


Fig. 8.—Section of a many-cell blastula (about × 8).

In a word, then, the segmentation of the ovum of Desmognathus is truly holoblastic, but the total cleavage is rather slow in appearing, and in the later stages of development the yolk mass becomes homogeneous by the disappearance of cell walls.

The Early Development of Dinophilus as Compared with that of the Annelids: James A. Nelson, University of Pennsylvania.—The ovum of Dinophilus segments into four cells, or macromeres, each of which gives rise by oblique alternating or "spiral" cleavages to five generations of smaller cells, or micromeres. The first three quartettes give rise to ectoderm. The posterior left hand member of the fourth quartette divides bilaterally and equally into two cells which later give rise to the mesoderm bands. The remaining cells give rise to the entoderm. This method of origin of the three germ layers is identical with that found in the Mollusca and the Polychæta. As in the two former groups the brain is formed from the first quartette, and the greater part of the trunk ectoderm from the posterior cell of the second quartette. In the details of the cleavage there is a striking agreement with that of the polychætous annelids. Cells arising from the first quartette identical in origin with the "primary trochoblasts" of the annelids, together with cells derived from the first and second quartettes, make up a cell row which very probably forms at least a part of the second ciliated band situated on the head of the adult, in a position corresponding with that of the prototroch of the annelid larva. Other details increase this resemblance. The symmetrical cell pattern known as "the cross" is formed by the same cells and at the same divisions as in the Polychæta, while in the divisions of the posterior cell of the second quartette bilateral symmetry appears at the same time and in the same cell as in several members of this group.

Such close agreement in the details of the cleavage, as well

as in the fate of the corresponding cells with the conditions obtaining among the Polychæta, speaks strongly for a genetic relationship between this group and the Dinophilidæ, since cleavage patterns are inheritable, as well as other characters.

Organ-forming Germ Regions in the Eggs of Ascidians and Snails: Edwin G. Conklin, University of Pennsylvania.—The early development of ascidians and snails is of such a determinate character, even in the earliest cleavage stages, that it seems probable that a definite polarity and localization of materials exists in the unsegmented egg. A study of the eggs of these animals shows that this antecedent probability is realized in fact.

In the living eggs of the fresh water snails, Limnæa, Physa and Planorbis, one may readily observe the segregation of unlike materials of the egg before cleavage begins. Before maturation the nucleus can be seen in such eggs as a large, clear vesicle, while the rest of the egg substance is filled with yolk granules and is yellow in color. During the maturation divisions the nuclear vesicle is dissolved and its contents form a clear area surrounding the polar amphiasters. After the second polar body is formed this clear area spreads out as a disk and then as a cap which covers the upper two-thirds of the egg. The lower third of the egg which is not covered by this cap of clear protoplasm remains of a bright yellow color. These two portions remain distinct throughout the subsequent development, the clear area giving rise to the ectoderm and the yellow one to the endoderm and mesoderm. In these snails, therefore, the germ layers are visibly outlined in the unsegmented egg.

A somewhat similar localization of germinal materials, before cleavage, occurs in the eggs of certain ascidians. In *Cynthia* (*Styela*) *partita*, *Ciona intestinalis* and *Molgula manhattensis* the central yolk mass of the immature egg is surrounded on all sides by a peripheral layer of protoplasm. In the living eggs of Cynthia the central yolk is gray in color while the peripheral layer contains granules of yellow pigment; in Ciona the yolk is red, the peripheral layer clear and transparent; in Molgula the yolk is gray, the peripheral layer clear. As soon as a sperma-

tozoon enters the egg this peripheral layer, together with the nuclear sap from the germinal vesicle, flows rapidly to the lower pole, at which point the sperm always enters. The yolk is left uncovered at the upper pole and here both polar bodies are formed. The protoplasm at the lower pole then moves up to a position just below the equator on the posterior side of the egg; and here the pronuclei meet and the first cleavage spindle arises. At the close of the first cleavage the greater part of the clear protoplasm moves into the upper hemisphere while the gray, yolk-laden protoplasm is largely collected in the lower hemisphere. In Cynthia the yellow pigment collects into a brilliant crescent, just below the equator on the posterior side of the egg; in Ciona and Molgula this crescent is clear and almost colorless. Owing to its color in Cynthia the substance of this crescent can be traced through the whole development until it gives rise to the muscle cells and the mesenchyme of the tadpole. The gray substance of the unsegmented egg gives rise chiefly to the endoderm, while the transparent protoplasm goes principally into the ectoderm. In these eggs, therefore, there is not only a localization of the material of the three germ layers before cleavage, but all the axes of the future animal are clearly established in the unsegmented egg.

An Experimental Examination of the Germ Regions of the Molluscan Egg: Edmund B. Wilson, Columbia University.—No abstract.

Polarity and Axial Heteromorphosis: T. H. Morgan, Bryn Mawr College. — The reversal of the polarity that is seen in axial heteromorphosis appears to give us an opportunity for an examination of the phenomenon of polarity itself, for, if we could determine the conditions that determine this reversal we might hope to gain some insight into the factors that determine the polarity. It is from this point of view that I offer the following observations on two species of planarians, *Planaria maculata* and *P. lugubris*.

If a planarian is cut in two at almost any level a new tail regenerates on the posterior end of the anterior piece and a new

head on the anterior end of the posterior piece. It appears that the same material is doubly potent, being able at nearly every level to form a head or a tail. Something in the piece itself determines that a head shall develop at the anterior cut surface and a tail at a posterior cut surface. This "something" is what we call polarity.

I have found certain exceptions in the planarians to this rule. Occasionally a cross-piece develops a head at each end, and in *Planaria lugubris*, especially, when the tip of the old head is cut off just behind the eyes, another reversed head regenerates from its posterior cut surface.

In the few cases in which I got double-headed forms I was impressed by the fact that this occurred only when the cross-pieces were very short, and never occurred in long cross-pieces. This lead me to try making the pieces very short in order to see if I could obtain in this way more of these double-headed forms. This I found to be the case, and I have obtained from such pieces double-headed forms from every part of the body of *Planaria maculata*. It is clear, therefore, that the result can not be connected with the presence of any particular structure at the cut end. A number of different kinds of experiments, mainly with pieces having obliquely cut ends, seemed to show that the main factor in the production of the heteromorphic head is connected with the shortness of the piece. I suggest as a tentative hypothesis that this shortening of the piece reduces the strength of the polarity so that it comes to have less influence on the new part than certain innate tendencies of the material itself. There is reason to conclude, as I have stated, that the new material that develops over the cut surface has the power of producing either a head or a tail. If now the polarity is reduced, or removed, that one of these two tendencies which is stronger will have a chance to assert itself. In the case of *Planaria maculata* the tendency to produce a head seems stronger than the tendency to produce a tail, hence the appearance of the heteromorphic head in the short cross-pieces, in which the polar influences fail to act. This conclusion I hold subject to future revision when we have gained more light as to the nature of the so-called polarity itself.

In *Planaria lugubris* I had found that when the head is cut off just behind the eyes a heteromorphic head is produced on the posterior end of the old head. From this result I confess that I anticipated that in this worm it would be even easier than in *P. maculata* to obtain double-headed forms from short cross-pieces. To my surprise I found on the contrary that these double-headed forms do not arise except in a few cases in which the cross-pieces have come from the region immediately behind the old head. Most of the other short cross-pieces produce a head and a tail, but in a small number of cases the structure that develops at the anterior end appears to be a tail. It would be difficult to determine with absolute certainty whether this anterior pointed structure is a heteromorphic tail or an undeveloped head, unless the pharynx were to develop. In one case a pharynx appeared in the new part at the anterior end, and another in the new part at the posterior end. In both the new pharynx pointed outwards, *i. e.*, towards the tip of the new part, hence there can be little question that the new structure is really a heteromorphic tail.

It appears in *Planaria lugubris* that while the material at every level has the double potency of producing a head or a tail according to which end of the piece it comes to lie at, yet in very short pieces from the middle and posterior regions of the body a double-tailed form may arise. We must suppose, therefore, on our hypothesis, that while in this species also the material is totipotent, yet when the determining influence of the polarity is removed the stronger tendency is to produce a tail, while in *Planaria maculata*, as we have seen, the stronger tendency is in the other direction.

In *Planaria lugubris* it has been necessary to assume that the most anterior part of the body has a different predisposition than has the rest of the body, since in the former a double-headed piece may develop and in the latter a double-tailed form. This result finds a parallel in certain other cases that I have observed in the earthworm and tadpole.

If an earthworm is cut in two behind the region of the gizzard there often develops from the anterior cut surface of the posterior piece of the worm a heteromorphic tail. In this case the

posterior part of the worm is not a short piece, and yet it is worthy of note that this region has practically the same structure throughout. This may mean that the conditions are fundamentally the same as those in the short cross-pieces of the planarian, and if so this may throw some light on the phenomenon of polarity itself.

It has also been shown in the earthworm by Hazen that from the posterior cut surface of a short piece of the head end a heteromorphic head may develop. Here we must assume that the tissues are predisposed to form a head, while in the posterior region they are predisposed to form a tail, and in both when the polar influences are removed these structures appear. It has been shown by Harrison in the tadpole that a tail-like outgrowth develops from the anterior cut surface of the tail. I have tried to show that this outgrowth is really a heteromorphic tail. Here again it is noticeable that the old tail has practically the same structure throughout, hence possibly, as in the earthworm, there may be a decrease in the polarity and the consequent development of a heteromorphic structure.

These considerations are tentative, and possibly premature: but the facts give us at least some grounds for the hope that the problem of polarity may not be beyond the reach of further analysis.

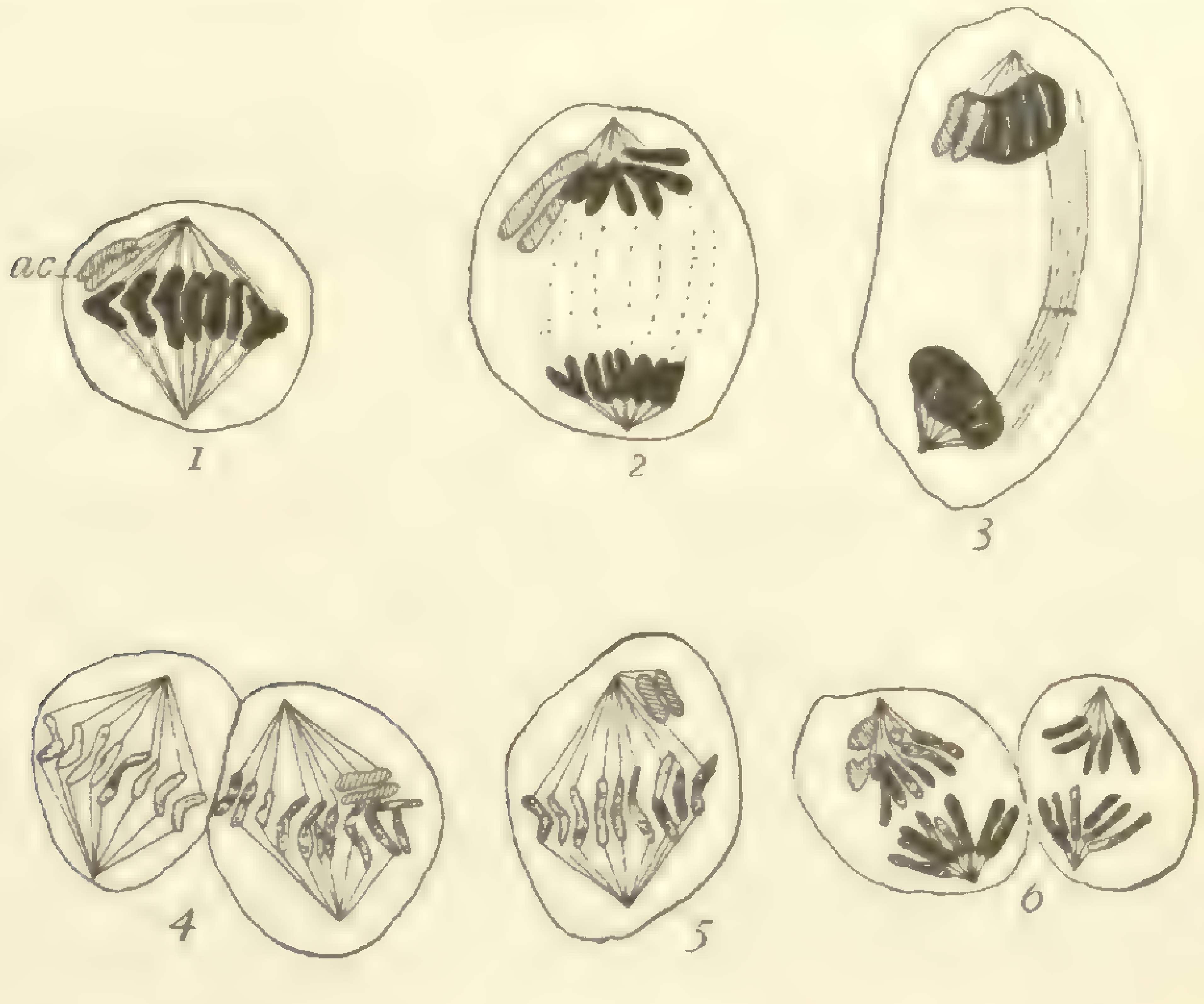
The Development of the Germ Layers in a Nudibranch Mollusc: Dana B. Casteel, University of Pennsylvania. — The cleavage of the egg of the nudibranch, *Fiona marina*, is of the spiral type well known for molluscs. From the mesentomere (4 d) arises the primary mesoblast and also enteroblasts, these latter being concerned in the formation of the intestine. Secondary mesoblast is formed from the third quartet of ectomeres in a manner similar to its formation in Physa and Planorbis. Two cells in each anterior quadrant sink below the surface into the cleavage cavity and by division there form two bands of cells on the sides of the anterior end of the gastrula. These elements later take part in the formation of the muscles of the velum, a larval organ, and are thus truly "larval" in character.

The anal excretory organ, characteristic of opisthobranch

larvæ, is undoubtedly of ectodermal origin in Fiona. It arises from one large and several small third quartet cells of the right posterior quadrant which, after torsion begins, are carried farther to the right side and above the anal opening. The larva also possesses additional organs of excretion, two in number, lying bilaterally in the anterior region of the body cavity. These, the "nephrocysts," are composed of but a few large vacuolated cells which contain concretions and fluid excreta. The origin of these cells has not been determined definitely, but they are probably derived from the mesoderm.

A Pair of Giant Nerve Cells of the Squid: Leonard W. Williams, Brown University. — No abstract.

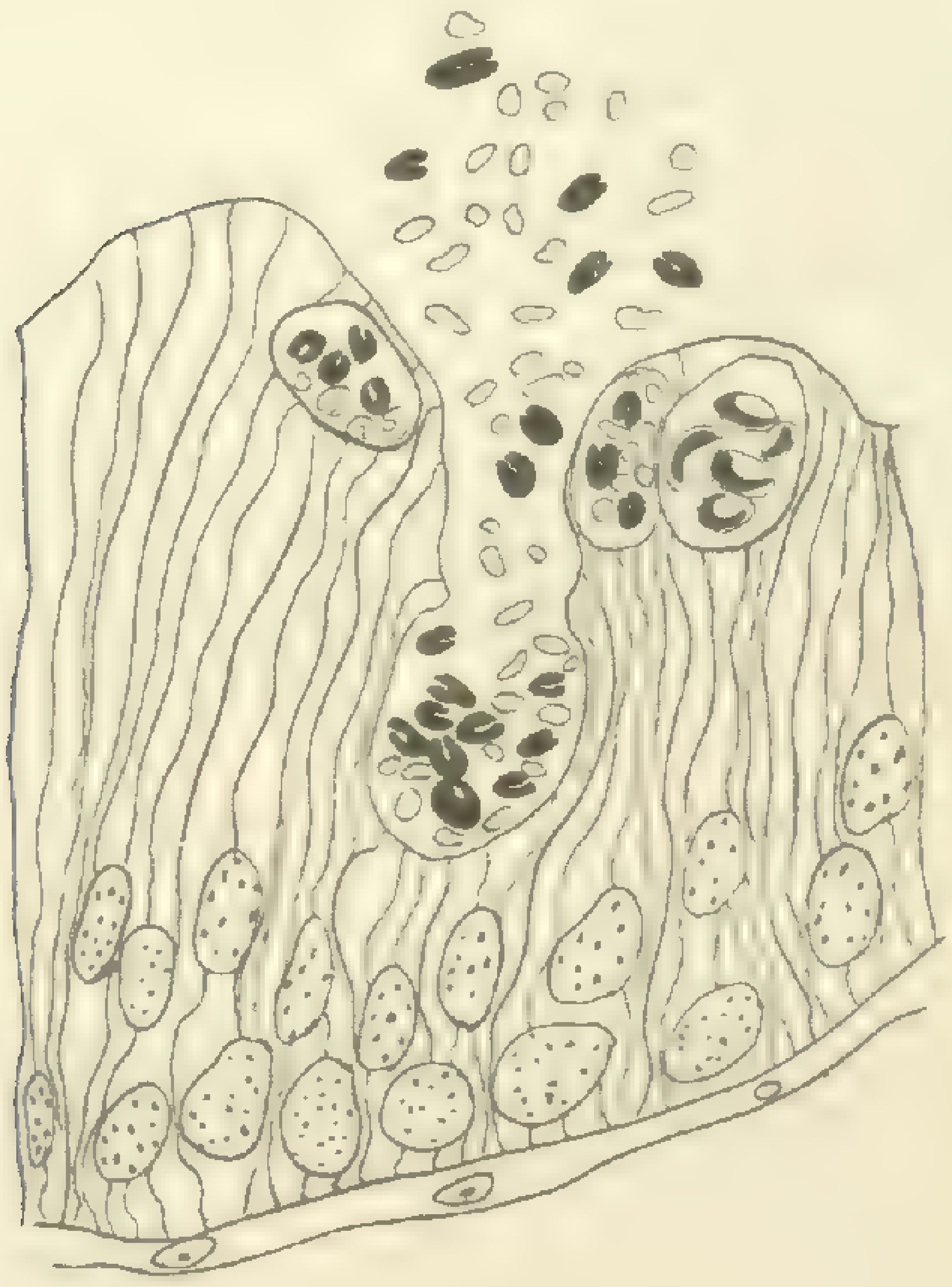
The Function of the Accessory Chromosome in the Spider: Louise B. Wallace, University of Pennsylvania.— In the spermatogenesis of insects a number of authors have described a



peculiar chromosome which has been called by various names. While these all agree in being unlike the ordinary chromosome, there seems to be sufficient disagreement to subdivide them into two groups. Montgomery's "chromatin nucleolus" and Paulmier's "small chromosome" are probably homologous and these authors have suggested that they may represent degenerating chromatin. McClung's "accessory chromosome" in Orthoptera

is too well developed to allow of such an explanation and since it divides in the second maturation division only and is thus distributed to but one-half of the spermatids, he regards it as a sex-determinant.

In the spider *Agalena nævia*, the peculiar chromosome closely resembles the one described by McClung and therefore I adopt his term but my results differ from his in regard to its distribution. I am convinced that, although split longitudinally, it takes part in neither of the maturation divisions and that, therefore, only one-*fourth* of the resulting spermatids possesses it. Such a condition would hardly favor the idea of sex-determination. Figures 1, 2 and 3 show spermatocytes of the first maturation division and Figures 4, 5 and 6, spermatocytes of the second maturation division.



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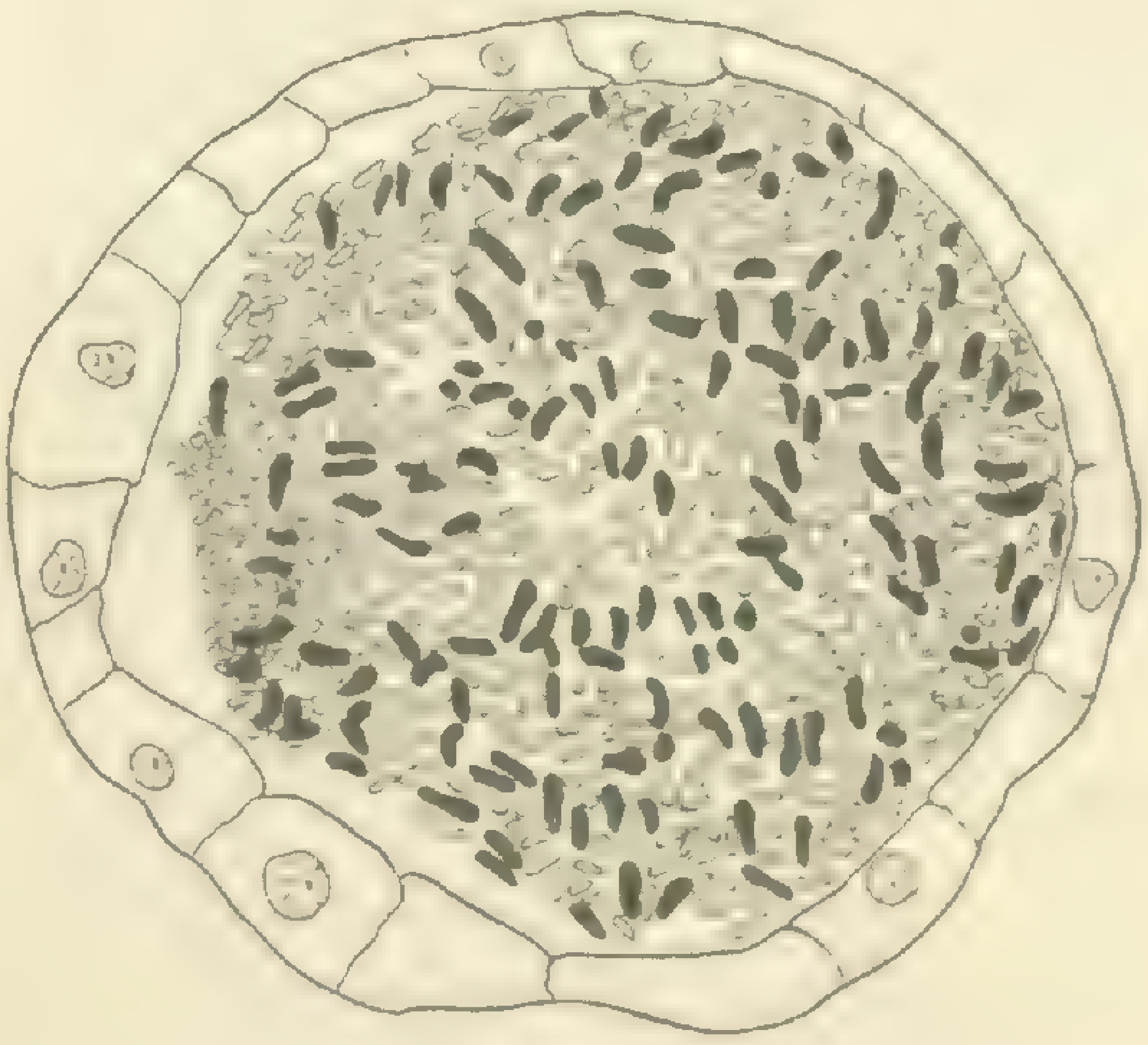

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In nests of maturing spermatozoa are found cells undergoing degeneration (Fig. 7) and these occur in great numbers in the testis and also in the ducts (Fig. 8) together with the much smaller number of ripe spermatozoa. This fact leads me to suggest that possibly only those spermatids which contain the accessory chromosome develop into functional spermatozoa and that the remaining three-fourths never reach maturity. If this interpretation be a true one, a parallelism could be drawn between the development of the spermatozoön and of the ovum, since in the latter only one of the four oötids develops into a ripe ovum,

the other three being thrown off as polar bodies and later degenerating.

The Lamellibranch Nervous System: Gilman A. Drew, University of Maine.— The nervous system of the giant scallop, *Pecten tennicostatus*, is greatly specialized, and the size of the animal makes it possible to study it by dissection as well as by serial sections. The cerebral and pedal ganglia are small, owing no doubt to the reduction of the parts they supply, and the visceral ganglia, supplying the large adductor muscle and sending a large number of nerves to the borders of the mantle, are very large and composed of distinctly marked regions. The pallial nerves that follow along the borders of the mantle lobes near the bases of the tentacles and eyes, present the structure of ganglia and supply nerves to the tentacles and eyes, which are very abundant in this form. The need for such ganglia is apparent, and their presence instead of a further complication of the visceral or cerebral ganglia indicates the ease with which such centers may be established when need arises.

The fact that the pallial nerves, that here show the structure of ganglia, are joined at intervals for nearly their whole length by nerves from the visceral ganglia, while only a very few nerves are sent to them from the cerebral ganglia, and these only to their extreme anterior ends, is taken as an indication that the loss during development of the anterior adductor muscle is accompanied by a suspension in the growth of other anterior portions, and that the bulk of the animal if formed by the excessive growth of the posterior portions.

The relation of the nervous systems of other lamellibranchs was also discussed.

The Early Stages in the Development of Ophiothrix Fragilis: E. W. MacBride, McGill University.— Comparatively few and scattered notices are to be found in zoölogical literature with reference to the early development of Ophiuridea and in a preliminary notice like the present communication, it will only be necessary to refer to one of them. In 1891 Russo[1] published

[1] Le prime fasi di sviluppo nell' Amphiura squamata — *Bollettino della Società in Naturaliste* in Napoli. Vol. 5, 1891.

an account of the formation of the layers in the embryo of the viviparous *Amphiura squamata*; and in that paper he made the startling statement that in *Amphiura squamata* the endoderm was formed by delamination from the inner ends of cells forming the wall of a hollow blastula, and that, further, the cœlomic sacs appeared as cleavage spaces in the midst of masses of mesenchyme cells.

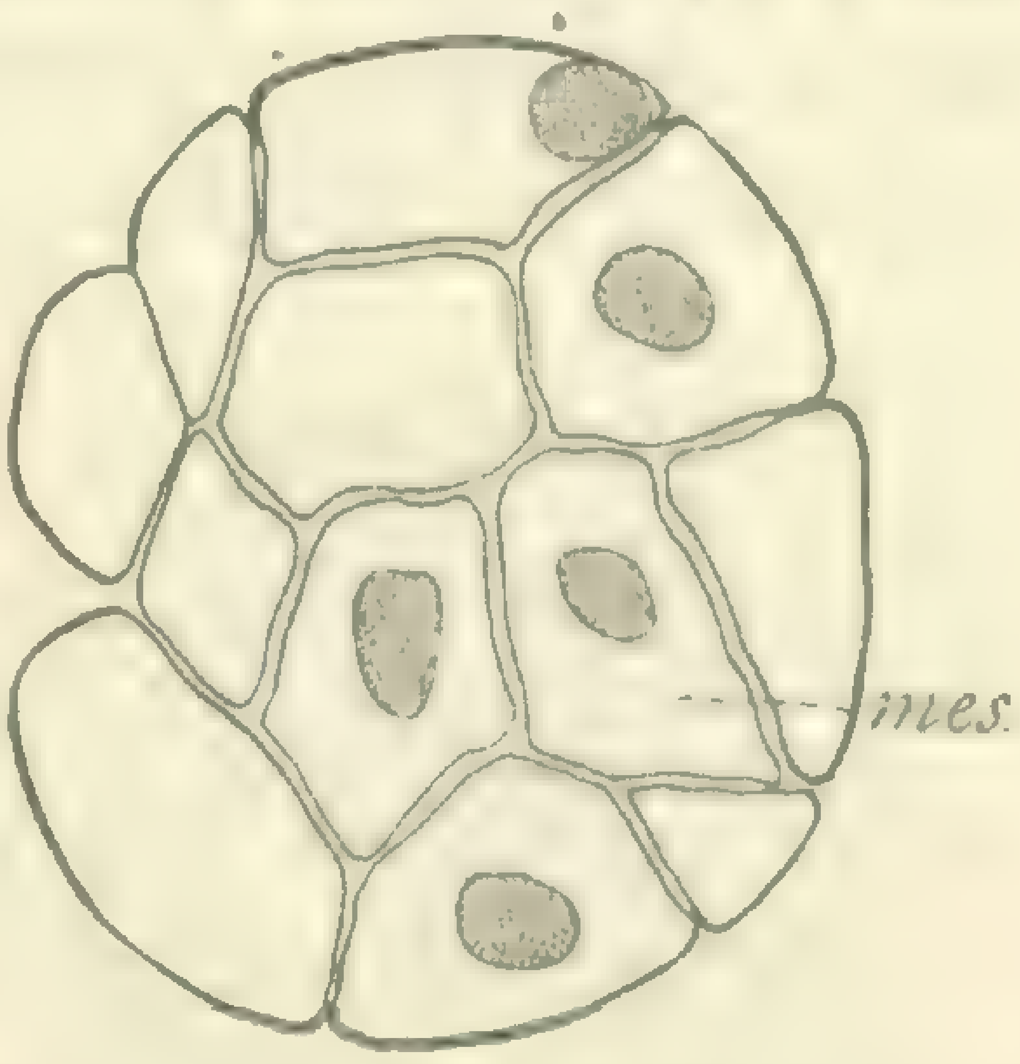

FIG. 1.—Section through the segmenting egg *mes.*, internal cells separated by tangential division.

Such fundamental differences between the developmental processes in this form and those in all other Echinodermata, were hardly to be credited without ample confirmation, especially when it is recollected that Amphiura squamata is not a favorable object for study owing to the difficulty of obtaining the earlier stages in quantity.

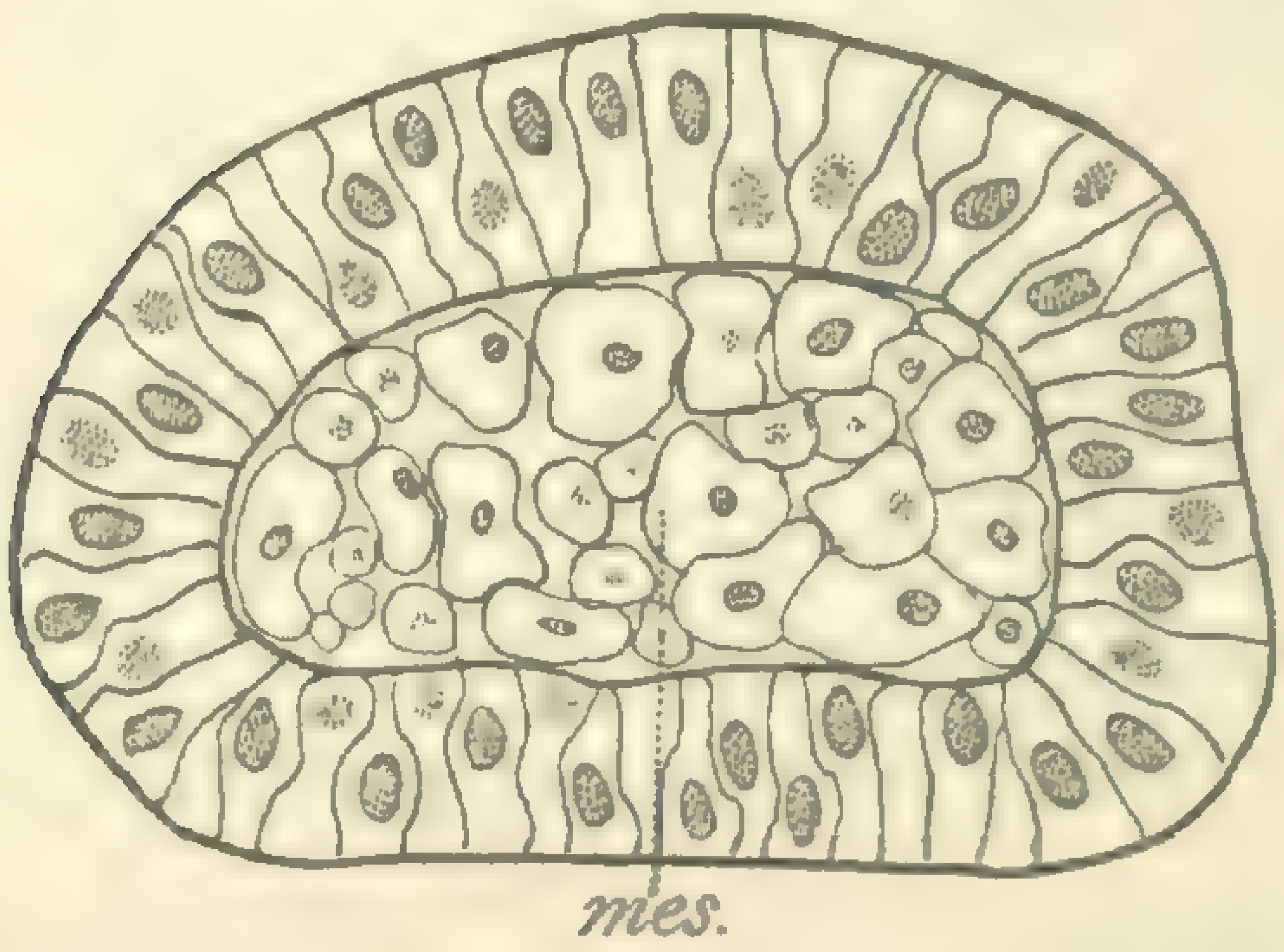

FIG. 2.—Section through embryo at the close of segmentation.

For this reason I selected the common British form, *Ophiothrix ragilis* for study, and, during a visit to the Plymouth Biological Station in 1898 I artificially fertilized a number of the eggs and reared some of the larvæ through the entire period of development up to and including the metamorphoses, the whole occupying about three weeks.

The egg of *Ophiothrix fragilis* is very minute, being less than .1 mm. in diameter, and is quite opaque so that in order to follow the earlier stages of development it is necessary to use serial sections.

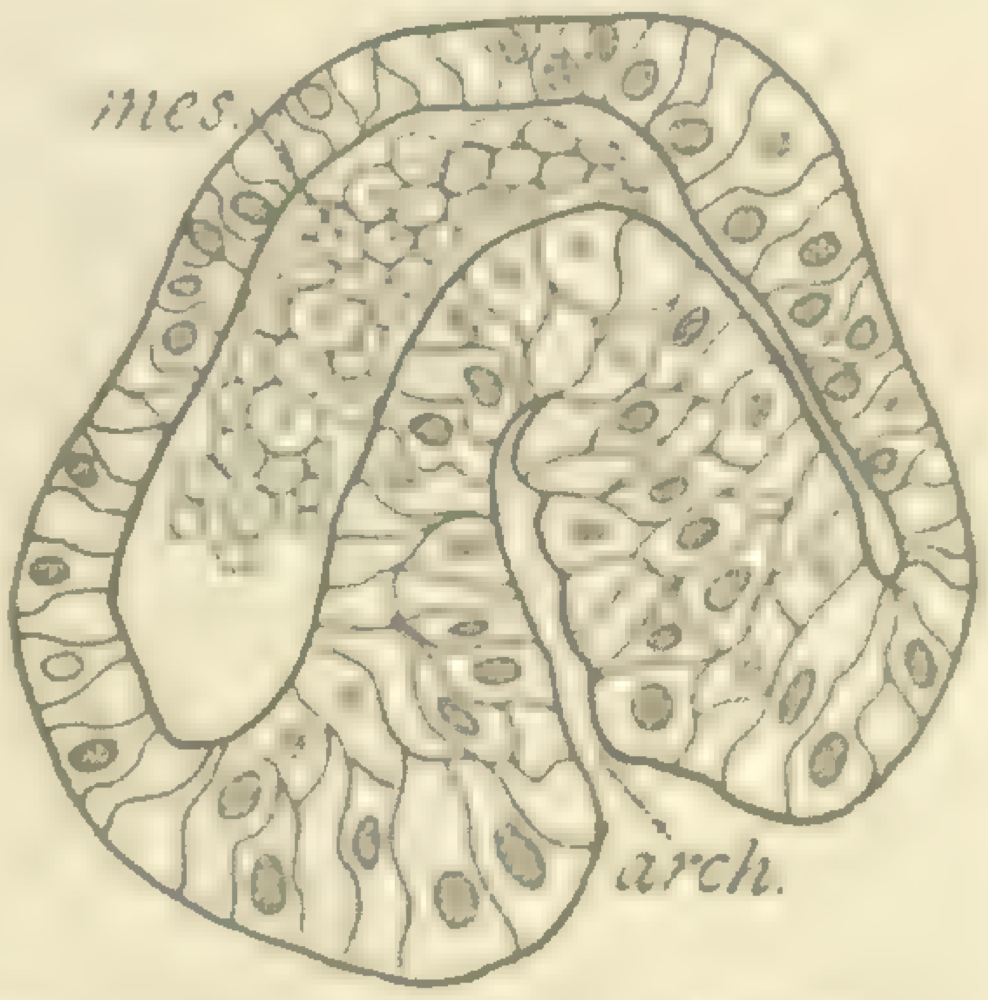

FIG. 3.—Longitudinal section of young gastrula *arch.*, archenteron.

As shown in Figure 1, the result of segmentation is not as in other Echinodermata, a hollow blastula, but a solid morula. From a comparison with one

another of my preparations, it appears that the egg at first divides into a few blastomeres, which are arranged around a vestigial, or perhaps we might say virtual blastocœle, and that as development proceeds this blastocœle swells but is kept continually filled by cells produced by tangential divisions of the peripheral blastomeres. At the conclusion of segmentation, the embryo strikingly recells a cœlenterate planula, as shown in Figure 2.

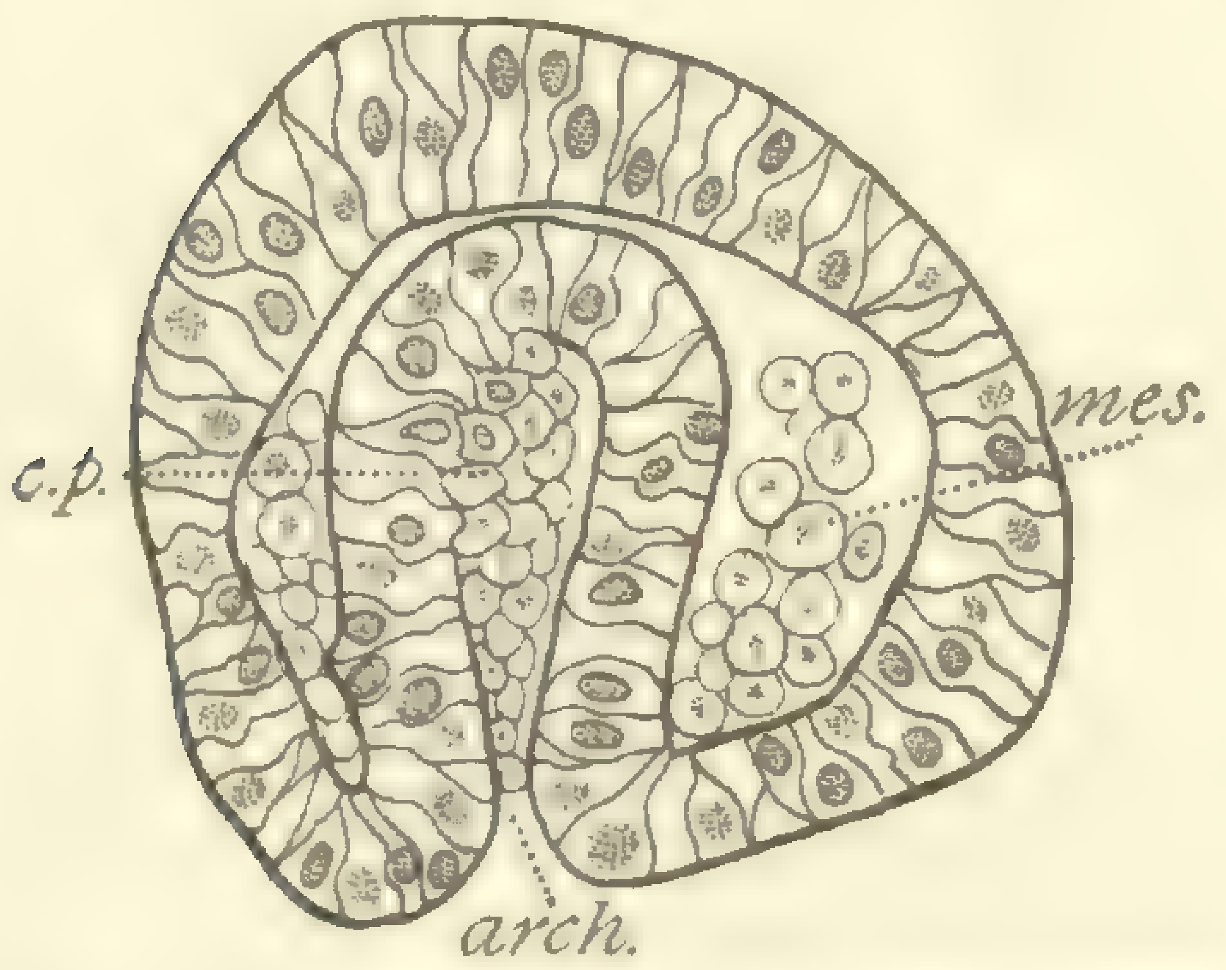

FIG. 4.—Longitudinal section of older gastrula *arch.*, archenteron *c. p.*, cellular plug.

The interior mass of rounded cells, however, does not constitute the endoderm, for, in the next stage (Fig. 3) a regular invagination has made its appearance, giving rise to an archenteron, which is, however, two or three cells thick on one side. The interior cells of the former stage are seen to occupy the space between archenteron and ectoderm, homologous with the segmentation cavity of other forms. In the completed gastrula

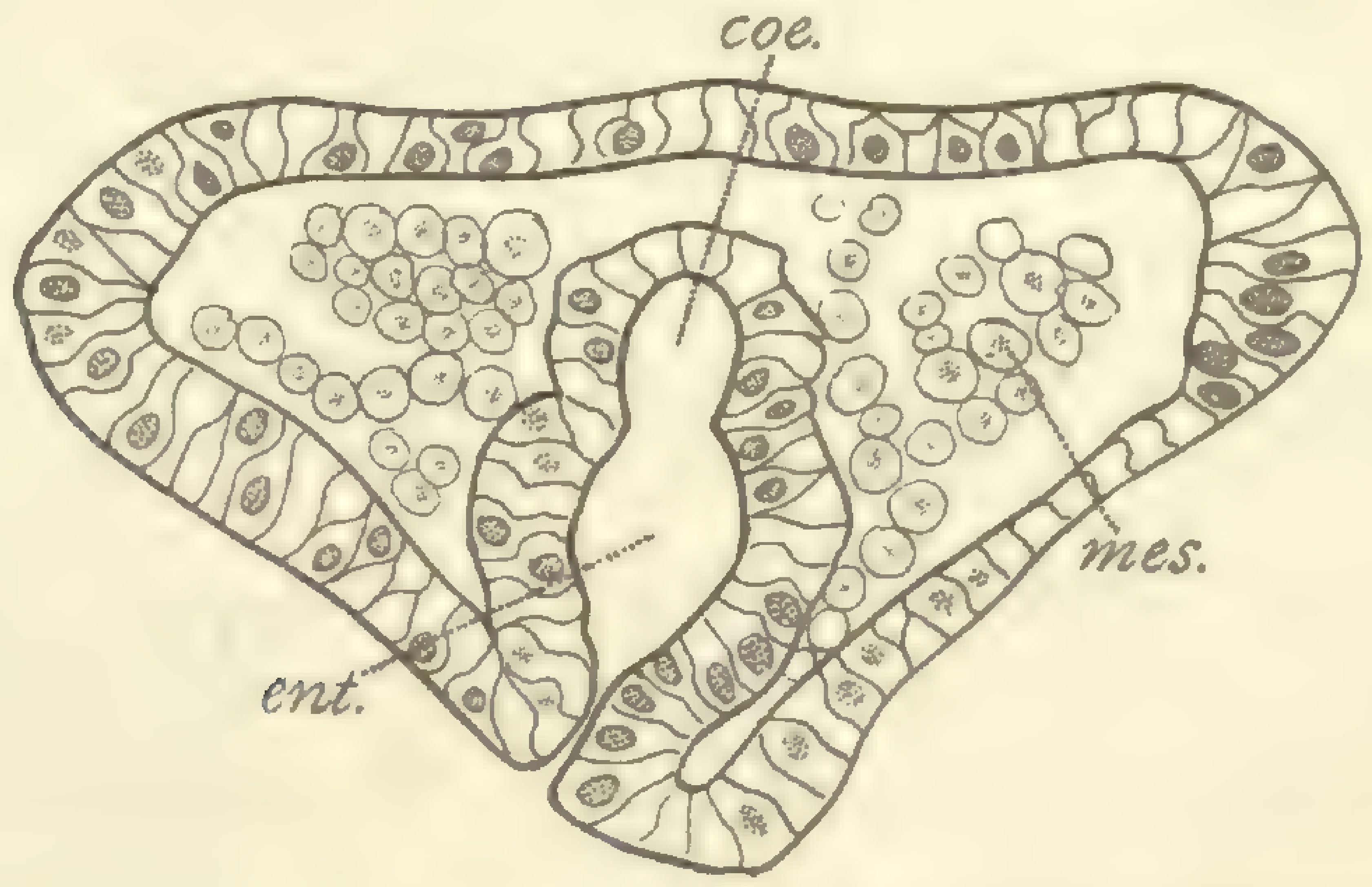

FIG. 5.—Longitudinal section through an embryo two davs old *cœ.*, cœlom *ent.*, enteron.

a curious plug of cells is seen projecting into the archenteron which is no doubt the remains of the thickened side of the archenteron of the younger gastrula (Fig. 4).

When the embryo has attained the age of two days, the rudiment of the cœlom appears as a vesicle at the anterior end of the archenteron exactly as it does in the embryos of Asteroidea. At the same time the embryo takes on a shape which may be

described as roughly triangular. The two basal angles of a triangle (Fig. 5) are really the rudiments of the first two arms of the larva, which throughout the whole larval existence are much longer than the rest, and are the most important organs of locomotion. The cells which form the interior mass at the close of segmentation are now seen to be destined to form the supporting calcareous rods for these arms, and hence we may attribute the leading peculiarity of the development, *viz.*: the appearance of a solid morula instead of a hollow blastula, to the extremely precocious formation of the skeletogenous cells for these arms.

On the Homologies of the Archenteron and Blastopore in Vertebrates: Charles S. Minot, Harvard University. — No abstract.

Medusa Fauna of the Bahamas: Alfred Goldsborough Mayer, Brooklyn Institute of Arts and Sciences.— The medusa fauna of the Bahamas is poor in comparison with that of the Tortugas, Florida. The writer secured ninety (90) species of Hydromedusæ, Scyphomedusæ, Siphonophoræ and Ctenophoræ at the Tortugas, while only forty-three (43) species were found at the Bahamas. What is more interesting, the relative abundance of specific forms is quite different in the two regions. The commonest medusa during the summer months at the Tortugas, *Pseudoclytia pentata*, is not found at the Bahamas, and the commonest medusa during the summer months at the Bahamas, *Lymnorea alexandri*, is not found at the Tortugas.

Altogether, of the forty-three species of Bahama medusæ, twenty-three (23) are about equally abundant on the other side of the Gulf Stream at the Tortugas. Sixteen are more abundant at the Bahamas than at the Tortugas, while four are more abundant at the Tortugas. This is accounted for by the following facts: The Tortugas lie to leeward of the Gulf Stream and the extraordinarily rich pelagic life of the great current is constantly driven upon their shores, while the Bahamas lie to the windward of the stream and their local fauna is not reinforced by creatures characteristic of the great current. There is, however, something more than a mere concentration of individ-

uals at the Tortugas, for a surprising number of characteristic species appear to be confined to this region alone. Moreover, at the Tortugas, we have a small land mass surrounded by pure deep ocean water, while at the Bahamas we find a vast area of shallow flats covered mainly by coralline mud, forming veritable submarine deserts covered only with a sparce growth of coralline algæ and a few scattered clusters of coral reefs and gorgonians. The water over these shallow banks is almost as deficient in life as is that of the desert bottom itself, very few Sagittæ, Salpæ or Crustacea being found, and among the Medusæ only representatives of the Gonionemidæ and Lymnorea are abundant. Indeed, the water of these shallow banks is usually charged with a flocculent mass of silt which adheres to pelagic animals, and appears to be rapidly fatal to them. The deep water regions of the Bahamas, however, such as the tongue of the ocean, or the water to the eastward of Great Abaco Island, are rich in pelagic animals which appear to be free from silt and in good condition. This water of the deep areas must, however, be often driven over the shallow banks by the winds, and its life be thus destroyed.

It is found that Olindias is closely related to Gonionemus, for in its ontogeny it passes through a stage in which all of the tentacles arise from the side of the bell, and are sucker-bearing as in Gonionemus. *Eucheilota paradoxica* is the only Leptomedusa known which produces an asexual generation of Medusæ by a direct process of budding. These daughter Medusæ are derived from both ectoderm and entoderm of the gonad of the parent, as is the case in the Sarsiadæ and in Hydroids. On the other hand, the Medusæ buds found upon the manubrium of *Bougainvillia niobe* are developed entirely within the ectoderm, the entoderm remaining inert and passive during the growth of the bud, its limiting membrane being unbroken, and no connection ever being established between the gastro-vascular cavities of the bud and the parent. In *B. niobe*, however, the ectoderm of the manubrium is of considerable thickness, affording abundant material for the formation of the bud. It is possible, therefore, that this peculiar method of formation of medusa buds from the ectoderm, which has been observed in *B. niobe* by

us, and in *Rathkea octopuncta* and *Lizzia clappadei* by Chun, may be due to a gradual process favored by the thickness of the ectoderm which may have prevented the deep-lying entoderm from taking an equal share in the formation of the bud until finally it has come to remain passive throughout the period of formation of the bud, as in *B. niobe*.

Medusæ produced from ectoderm alone may, therefore, be phylogenitally homologous with Medusæ produced by the more primitive and universal coöperation of both ectoderm and entoderm.

Among the new forms discovered, *Parvanemus degeneratus* is the most degenerate free-swimming hydroid medusa yet described. It lacks tentacles, sense organs and peripheral vascular system. It swims, however, with great activity, but is short lived.

Correlation as the Basis for Selection in Lepidoptera: Henry E. Crampton, Columbia University.— Read by title.

Exhibition of a Cat, Showing Abnormal Placement of Viscera: C. M. Clapp, Mount Holyoke College.— No abstract.

The Origin and Function of the Medullary Sheaths of Nerve Fibres: Porter E. Sargent, Browne and Nichols School, Cambridge.— No abstract.

Demonstration of Pulsatile Anterior Lymph Hearts in Young Tadpoles: Henry McE. Knower, Johns Hopkins University.— No abstract.

Excretory Activities in the Nuclei of Gastropod Embryos:[1] O. C. Glaser, Johns Hopkins University.— The primitive urinary bodies of the larva of *Fasciolaria tulipa* attain great size and are very favorable objects for study. They originate as two pear-shaped patches of highly vacuolated ectoderm at the sides of the definitive mouth. On account of their connection with

[1] The material on which this work was done was collected during three summers in North Carolina. I am deeply indebted to the Hon. Geo. M. Bowers for the courtesies of the Beaufort Laboratory of the Bureau of Fisheries.

the velar fold they are later carried outwards from the wall of the embryo and ultimately hang down from the under side of the velum.

Between the two extremes in development mentioned, the cells composing these bodies increase in size, in number by addition, and undergo a period of active excretion. Early in this period the nuclei divide amitotically, and the cells become polynucleated. The nuclei are granular, very irregular in outline, and each one has at least one nucleolus surrounded by a clear area. In addition the cells are characterized by their highly vacuolated condition (Fig. 1).

In sections through these nuclei, before and after amitosis,

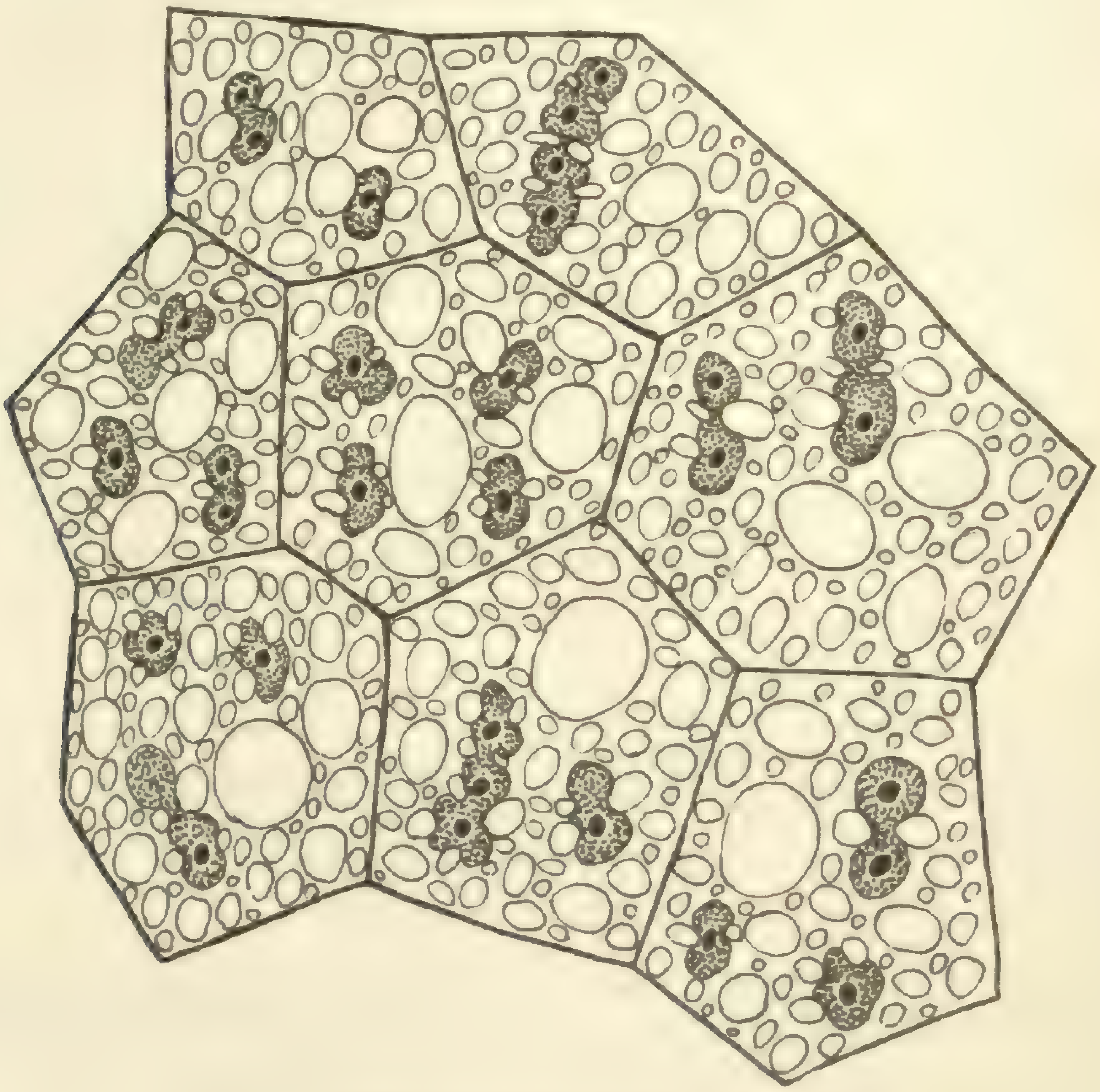

Fig. 1.— Surface view of part of external kidney.

the chromatin is arranged in an irregular network (Fig. 2 A, B, C). The nucleolus (*nl*) has a different staining reaction, and is probably a typical plasmosome. The halo surrounding it, instead of being circular or oval in outline, as it appears to be in whole mounts and in optical sections, is highly irregular, its outline projecting in finely attenuated processes into the body of

the nucleus. These processes are so delicate and the granules bounding them so small in comparison with the chromatin granules in the network, that they are invisible except in sections. The location of large chromatin granules continuous with the nuclear reticulum, in the indentations of the halo, explains its circular appearance in entire preparations, because these granules are the only parts of the outline visible. They also afford an explanation of the irregular outline itself, for if we imagine a sphere of liquid to proceed out from the nucleolus in all direc-

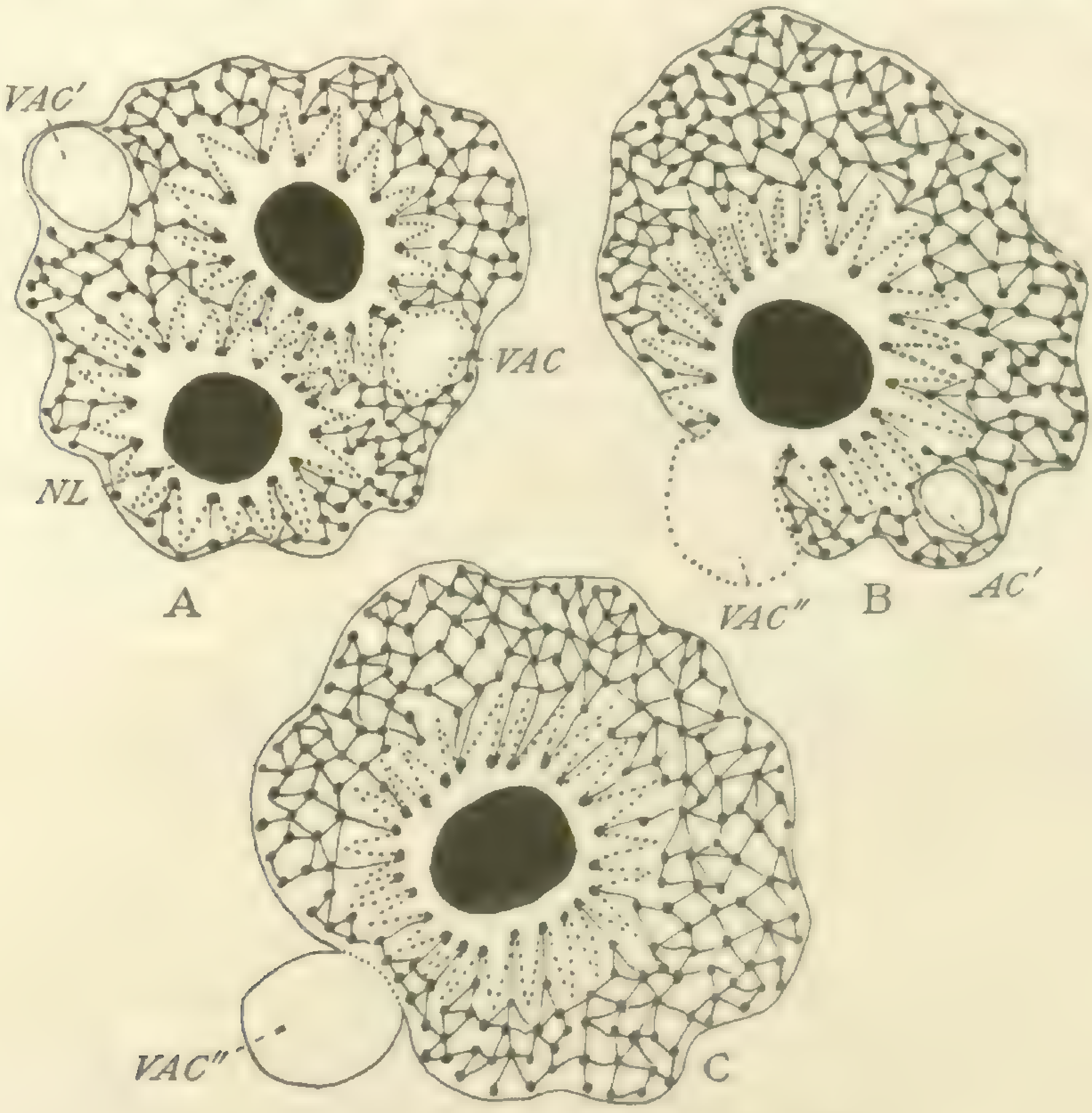

FIG. 2.—Sections of nuclei of excretory cells.

tions, any larger objects with which it might come in contact would, after yielding as much as possible, detain the surface at certain points, allowing it to advance only where there is no resistance, *viz.*, between the larger granules. In many cases the projections of the halo end distally in bulges or vacuoles (A, *vac*) which, apparently through the agency of the larger granules of the nuclear reticulum, become constricted off and may afterwards be found loose in the nucleus (A, B, *vac'*), from which they may finally escape (C, *vac''*). In other cases the projections of the halo may break through the wall of the nucleus before the vacuoles separate (B, *vac''*).

These phenomena strongly suggest an excretory activity, and this suggestion is strengthened by our knowledge of the behavior of amitotically dividing nuclei in other animals, but especially by the results of R. W. Hoffmann on the behavior of the nuclei and nucleoli in the large macromeres of the embryos of Nassa mutabilis. Complete proof, however, that the activities described in the sub-velar masses of Fasciolaria are really the exhibition of an excretory process, is found in a chemical analysis of an aqueous extract of these bodies. Such an extract analyzes like a dilute solution of urea.

Double Reproduction in the Medusa Hybocodon prolifer: H. F. Perkins, University of Vermont.— Hybocodon is familiar to American biologists as a singularly asymmetrical jelly-fish found along our coast in the early spring. Of the four radial canals only one is continued beyond the bell in a tentacle.

The method by which this medusa has been described as reproducing its kind is by developing, upon the bulbous base of this solitary tentacle, gemmiferous buds. These, when mature, become detached from the parent and swim away as free jelly-fish. Only the one tentacle is developed upon these buds, and at the time of liberation the base of this tentacle frequently carries maturing buds of a second generation.

While this is a rapid and efficient means of propagation, it is not the only one. In addition to this asexual process, a sexual process is also present. Eggs or sperms are produced within the gonads which surround the manubrium, and these develop within the tissue to the condition of tentacled actinula larvæ. Thus the adult Medusæ give origin to two sorts of offspring, one by gemmation, the other by sexual production of viviparous young. This in itself is not anything extraordinary, but it is a matter of interest that the two processes are found taking place simultaneously in the same individual, and that this coincidence does not lessen the rapidity with which the embryo jelly-fish are produced on the tentacle bulb. The fact is of interest only as showing that the reproductive activities of Medusæ are even more unrestricted than we have realized.

The sexually produced larvæ of Hybocodon mature upon the

wall of the parent manubrium, attached to this member, after the earliest stages, by a slender connecting stalk. Ten tentacles appear while the larva is still a spherical mass, and as they lengthen assume a direction pointing away from the point of attachment. The mouth and oral tentacles of the actinula are developed after liberation at the pole which was, during the attached period, next to the parent.

The Development of the Heart and Branchial Blood Vessels of Ceratodus: William E. Kellicott, Columbia University.— No abstract.

Regeneration in Scyphomedusæ: Chas. W. Hargitt, Syracuse University.— Notwithstanding the remarkable development and scope of experimental zoölogy during the past decade, extending to members of every phylum from Protozoa to Vertebrata, comparatively little has been done directly upon any of the Medusæ, and almost nothing upon Scyphomedusæ. The incidental reference of Haeckel to such a tendency among certain of these organisms is hardly more than a hint, with nothing whatsoever as to details. Such is also the case with the later work of Eimer and Romanes on the nervous system of the Medusæ, at least as it pertains to problems of regeneration, though painstaking and important in its bearings on problems of locomotion and co-ordinated activities. More recently Uexküll has also reviewed some of this work, and while differing in many respects from that of his predecessors as to conclusions, leaves untouched the subject of regeneration.

The series of experiments of which this abstract furnishes the barest outline was undertaken with a view to ascertain the comparative capacity of Scyphomedusæ to reproduce lost parts, such as bits of the various parts of the body which might be lost by the usual exigencies of the struggle of life. The experiments comprised some three phases of regenerative energy:— First, the general ability to recover from such injuries as rents of the umbrella, etc.; second, regeneration of such organs as oral appendages; third, ability to regenerate such specialized organs as the sensory bodies.

Concerning the first, it required but few experiments to determine very clearly the existence of such a capacity, though its progress was somewhat more slow than had been anticipated. Various rents of the umbrella were soon healed, but excisions of the margins of the body were regenerated much more slowly.

Concerning the second class, the responses were similarly slow. An excised oral arm required several weeks to completely regenerate, as was also the case with excised portions of the gastric pouches.

Concerning the third class I had entertained some doubt, namely the power to reproduce the more specialized organs, such as rhopalia or sensory bodies. The experiments were an agreeable disappointment, as these organs were quite as promptly regenerated, if not indeed more so than had been the case with the former. In some cases the first signs of regeneration were noted within five days of their excision, and in from eight to twelve days their functional power was clearly recovered, as was proved by details of experimentation impracticable to describe here. The associated organs, such as lappets, hood, etc., were also quite as fully regenerated as the other.

Histological examinations show beyond any doubt the operation of typical histogenic processes, various phases of the regenerating organ being easily traceable from stage to stage to perfect maturity of form and structure.

In earlier experiments of a similar sort made upon Cyanea and Aurelia by the writer it was found impossible to maintain the normal vitality of the animals for sufficient time to secure any conclusive results. Rhizostoma, however, lends itself most remarkably to experimentation of various sorts and for continuous periods of from four to six weeks without material loss of vigor or regenerative power. It was found, however, that this was somewhat dependent upon the size and, presumably, age of the specimens. Those of large size, 75 to 125 mm. in diameter, proving much less hardy under an aquarium environment than specimens of smaller size; though very small specimens also proved less satisfactory. Specimens of from 40 to 60 mm. in diameter proved much the better, not only from the apparently greater vigor, but also in convenience for experimentation and observation.

The experiments clearly prove the capacity among these organisms for regeneration of organs or parts of organs, from the more generalized sort to the most specialized, and that with approximately similar readiness.

A New Generic Type of Polygordidae: J. Percy Moore, University of Pennsylvania.—The annelid referred to is known only from a couple of fragmented specimens found in association with marine Oligochæta on Cape Cod. Like Polygordius it has a slender, elongated form, an acutely conical prostomium bearing a pair of prominent, slightly articulated, apical tentacles, a round, open mouth, and above it a pair of deep, ciliated, sensory pits. The segments are very obscurely indicated externally in the anterior region but are clearly defined at the caudal end. The body wall exhibits the same succession of layers as in Polygordius; and internally are found a similar digestive tract with eversible proboscis, divided of the cœlom by transverse intersegmental dissepiments and dorsal and ventral longitudinal mesenteries, an oblique muscle band supporting the metameric gonads, and an epidermal nervous system ending anteriorly in a bilobed cephalic ganglion. In all these and other characters the worm resembles Polygordius, but in three important respects differs from that genus.

By an arrangement which can be described as a shortening of the oblique muscle sheet, the thick layer of longitudinal muscles is folded on each side in the form of a longitudinal ventrolateral ridge in which the muscle fibres assume (in transverse section) a radial arrangement and undergo certain structural changes. Thus is approached the condition found in many of the more primitive Polychæta and the manner in which the segregation of the dorsal and ventral longitudinal muscle tracts of annelids may have occurred is indicated.

At the caudal end the last ten or twelve somites are setigerous. Two of these bear a pair of seta on each side but the others only a single slender, vitreous, capillary seta, which arises on each side from the place of insertion of the oblique muscle and curves over the back for a distance nearly equalling the diameter of this region.

The anal segment or pygidium shows no enlargement nor other peculiarities exhibited by most species of Polygordius. There are no marginal papillæ or special appendages of any sort, but the pygidium continues the general outline of the rest of the caudal region to the anus. The caudal setæ evidently serve the same purpose as the bulbous enlargement with its papillæ of Polygordius in anchoring the posterior end of the worm. For this worm the name of *Chætogordius canaliculatus* is proposed. Its chief interest is that it somewhat bridges the gap between Polygordius and the Polychæta and partially confirms the view expressed thirty years ago by McIntosh that Polygordius finds its nearest polychæte relations in the Opheliidæ.

The First Steps Toward Degeneration in the Parasitic Copepods: Charles B. Wilson, State Normal, Westfield, Mass.— No abstract.

Gymnandromorphous Ants; W. M. Wheeler, American Museum of Natural History.— No abstract.

Trematode Parasites of American Frogs: H. S. Pratt, Haverford College.— Up to the present time the following species of trematodes have been found in American frogs:— *Halipegus* (*Distomum*) *ovocaudatus* Vulpian in the mouth and eustachian recesses; *Hæmatolœchus* (*Distomum*) *longiflexus* Staf., *H. similiplexus* Staf., *H. breviplexus* Staf., *H. varioplexus* Staf., and *Ostiolum* (*Distomum*) *formosum* Pratt in the lungs; *Pleurogenes* (*Distomum arcanus* Nickerson encapsuled in the pylorus and the liver; *Distomum quietum* Staf. *Cephalogonimus americanus* Staf., D. retusum Leidy, and Holostomum nitidum Leidy, in the small intestine: *Diplodiscus* (*Amphistomum*) *subclavatus* Gœze in the rectum; *Gorgodera* (*Distomum*) *amplicava* Looss, *G. simplex* Looss, *G. attenuata* Staf., and *G. translucida* Staf., in the urinary bladder; *Distomum tetracystis* Gal. encapsuled in the muscles of the throat; and *Monostomum ornatum* Leidy in the body-cavity.

The Structure and Development of the Compound Eye of the

Bee: E. F. Phillips, University of Pennsylvania.—The ommatidia which make up the compound eye of the honey bee are each composed of a crystalline cone of four cells and a rhabdome surrounded by eight or occasionally nine retinular cells. Each ommatidium is sheathed by two kinds of pigment cells, the inner pigment cells, two in number which surround the base of the crystalline cone and the outer pigment cells, twelve in number which extend the entire length of the ommatidium. Each retinula cell sends in a process to the retinular ganglion which has the property of a nerve fibre. The nerve fibres of the eye are differentiated portions of the retinular cells which send in fine branches to the rhabdome, which is probably the nerve ending of the eye. There is no connection between the crystalline cone and the rhabdome and the cone has not a sensory function.

The ommatidia develop from a single layer of thickened hypodermis and the region of the compound eye is marked out in the unhatched larva. The first indication of ommatidia is the grouping of cells with a distinct boundary in young larvæ. The cells of these groups become differentiated until each group is composed of a spindle-shaped mass with large nuclei, surrounded by numerous cells with smaller nuclei. The central spindle forms the retinula and the rhabdome is early visible as a clear space at the outer surface. The crystalline cone arises from the sides of the retinula and the pigment cells are still farther out. The ommatidium is formed as a morphological invagination of the hypodermis as was held by Watase. The rhabdome and crystalline cone are formed as intracellular secretions and the lens is secreted by the inner pigment cells whose nuclei in the young pupal eye are distal to the cone and afterward migrate to the base of the cone.

THE ANATOMY OF THE CONIFERALES.

(*Continued from page 359*).

D. P. PENHALLOW.

Resinous Tracheids and Resin Cells.

The investigations of Eichler (11, p. 35) show that in Ginkgo the wood is characterized by the presence of wood parenchyma elements which take the form of short idioblasts of a lenticular form in longitudinal section, and are distinguished by the storage of crystals of calcium oxalate. These structures are peculiar to this genus in which they form a specific character of definite value, but a more detailed account of them at this time is not called for.

In a large proportion of the Coniferales the wood is characterized by the presence of more or less numerous wood-parenchyma cells. These are always distinguished by their cylindrical form and transverse terminations. They are invariably associated with the production of resin, either as entering into the composition of resin passages, or as isolated cells. It is this latter group with which we are most particularly concerned at the present moment and as, with very few exceptions, they are uniformly characterized by the presence of resin which gives them a distinctive appearance, I prefer to describe them as "resin cells" rather than by the more commonly employed designation of "wood-parenchyma," which conveys no suggestion of their special function and most prominent feature.

Before proceeding to consider these structures more in detail, it will be necessary to digress for a short time and discuss certain other elements which have been erroneously regarded as wood-parenchyma. It has been stated by Eichler (11, p. 35) that wood-parenchyma elements occur in Araucaria and Agathis, but this is evidently due to a wrong interpretation of certain features presented by species of those two genera, which, according to

our investigations, are wholly devoid of such structures, in the sense defined above.

In *Araucaria excelsa* a transverse section shows more or less numerous elements containing resin. These are not to be distinguished in their general structure from the surrounding tracheids, and they are to be recognized solely by their contents, which are usually somewhat prominent. Their distribution is characteristic. They occur in small, scattered groups, or more commonly in rows one or two elements wide, parallel with the medullary rays and in immediate contact with them on each side. When the plane of section passes near the position of the supposed terminal walls the latter may be seen to be cut through in various ways, but they never exhibit any structural features, and they are therefore in no way comparable with the terminal walls of the wood-parenchyma cells. In a radial section they are seen to be long and fusiform, exactly resembling the wood tracheids, except for a reddish brown transverse plate which occurs either close to or exactly opposite a medullary ray, a position which is more clearly shown in a tangential section (Fig. 35). The dark plates closely resemble Sanio's bands, for which they might very readily be mistaken upon casual observation, or they might likewise be mistaken for terminal and unpitted walls. In *Agathis australis* these features are represented in their typical form. The transverse section shows such elements to be numerous and disposed in radial rows on each side of the medullary ray (Fig. 32). In a radial section they present the same fibrous and fusiform character as in Araucaria, but in addition the wall usually experiences a marked increase in secondary growth within a region exactly opposite the ray (Fig.

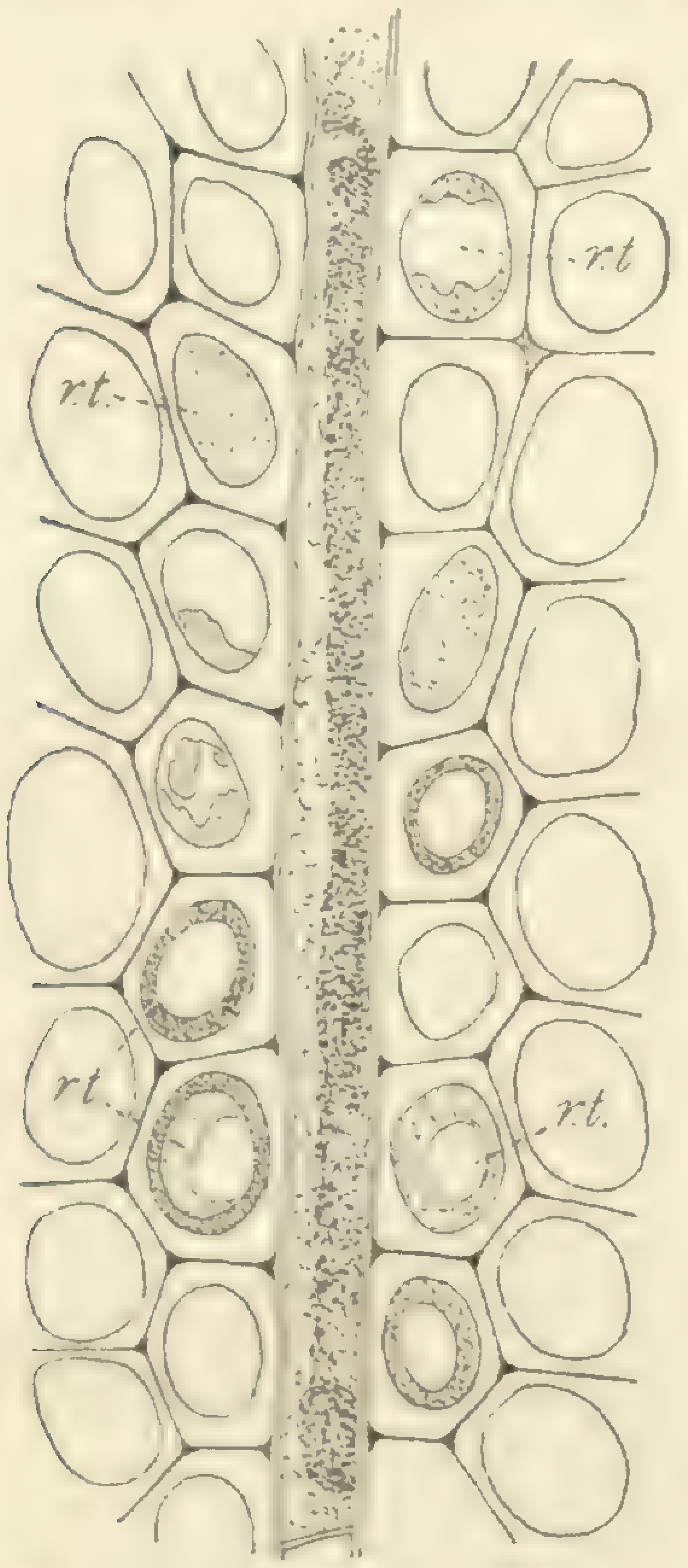

FIG. 32.—*Agathis australis*. Transverse section showing the disposition of the resinous tracheids on opposite sides of the medullary ray at *r. t.* × 300.

33). This feature is also prominent in a transverse section (Fig. 32). Such local increase in thickness always arises in adjacent cells in such a way that the more strongly thickened regions are exactly opposite, and they serve to constrict the cell cavity gradually from above and below in such a way as to leave a channel about half the usual width of the cell cavity, which gradually widens upward and downward (Fig. 33). It is at the position of maximum constriction that we find a transverse plate of variable thickness, but always of a reddish brown color. These plates are always thinnest in their central region, and they may be of uniform thickness for the greater part of their extent. At the region of contact with the tracheid wall they become thicker and thereby attain a vertical distribution to an extent four or five times greater than the general thickness. At such position also there is somewhat clear differentiation between the plate and the wall in point of color. Such plates show absolutely nothing of the nature of pits, and they are in no sense comparable with the terminal walls of the wood-parenchyma cells, except in form and position (Fig. 33).

The peculiar position of these plates, their resinous color and their simulation of both Sanio's bands and terminal walls, excited a suspicion as to their true nature and led to the belief that they might not be structural features at all. They were therefore subjected to a series of careful tests to determine (1) if they were structural, (2) if they were resinous, and (3) if the latter, to what extent. It was recalled in this connection that, although devoid of any special secretory reservoirs in the wood, Agathis is nevertheless well known for its production of the resin called gum dammar. It was suspected that the plates might be local deposits of resin, and they were therefore brought into direct comparison with gum dammar,

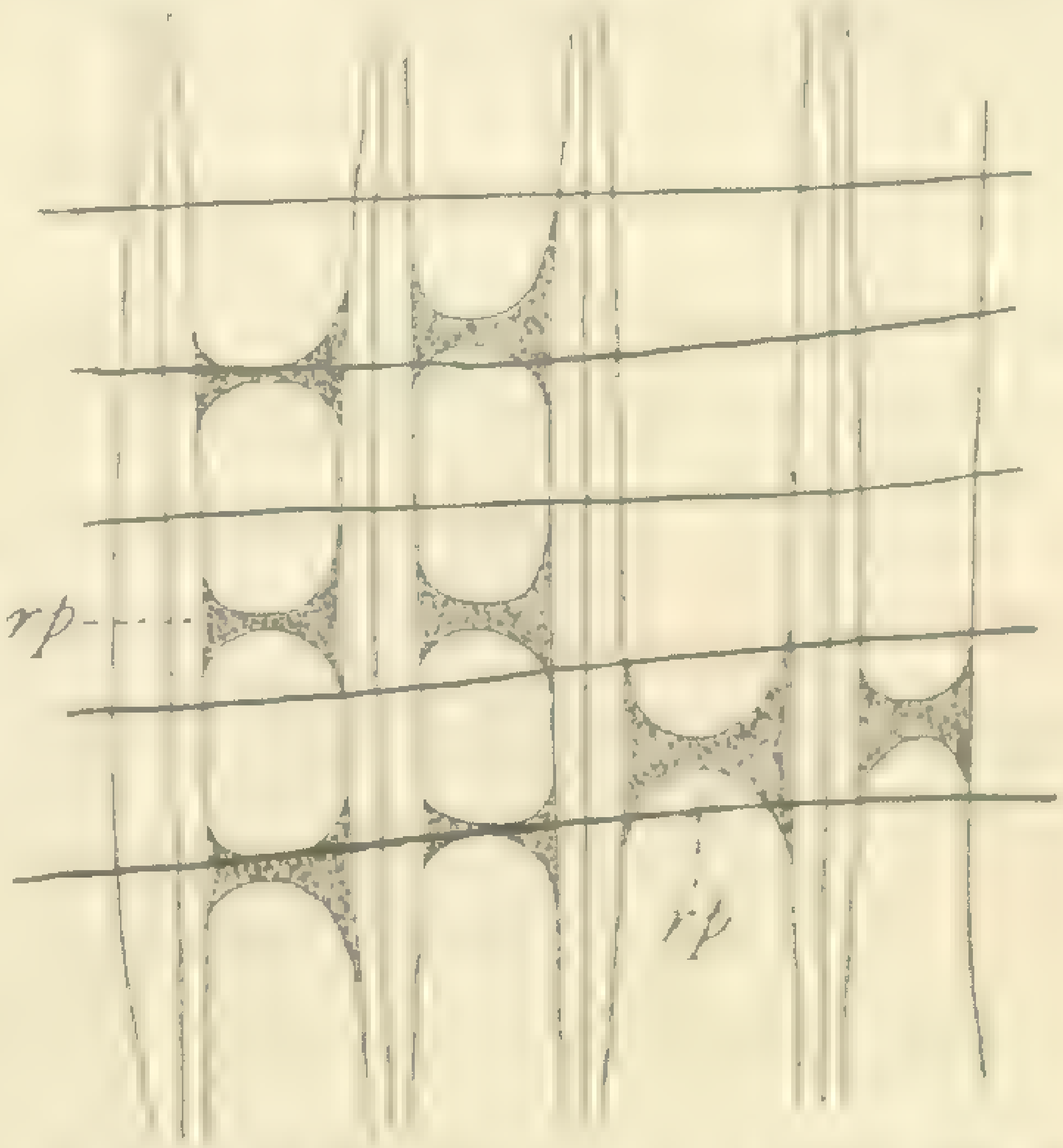

FIG. 33.—*Agathis australis*. Radial section showing the local thickening of the tracheid wall, and the occurrence of resin plates (*r. p*) opposite a medullary ray. × 225.

the characteristics of which are well known and described by Wittstein (D. 53, p. 63). Tests were applied to thin radial and tangential sections, employing for this purpose (1) various essential and fixed oils, (2) ether, (3) alcohol, (4) ammonia, (5) potassium hydrate in one and one half percentage solution. The plates were found to be very refractory with respect to both the fixed and essential oils, as well as towards ether, alcohol, ammonia and xylol, and in all of these cases no change was to be observed, even after an action extending over several weeks. A partial exception applies to alcohol and ether. In the latter case there did appear to be a certain diminution in volume, apparently through solution, when the reagent was first applied, but after that there was no further alteration. The application of alcohol, both in the hot and in the cold, showed that while the resin contained in the medullary rays was all dissolved, the plates were only partially affected. The reaction of the reagent was chiefly manifested in the development of strong curvature, often accompanied by fracture. This was evidently due to an increase in volume, and a tendency toward solution, and it gave the first definite evidence that the plates could not be of a cellulose character. Beyond this no further change was brought about, even after several weeks of action. The potassium hydrate gave the most positive results. At first there was no apparent change, but after an interval of about ten days or two weeks the plates were found to have completely disappeared, leaving a perfectly clear channel in the cell cavity. A further proof of the resinous character of these plates is to be found in

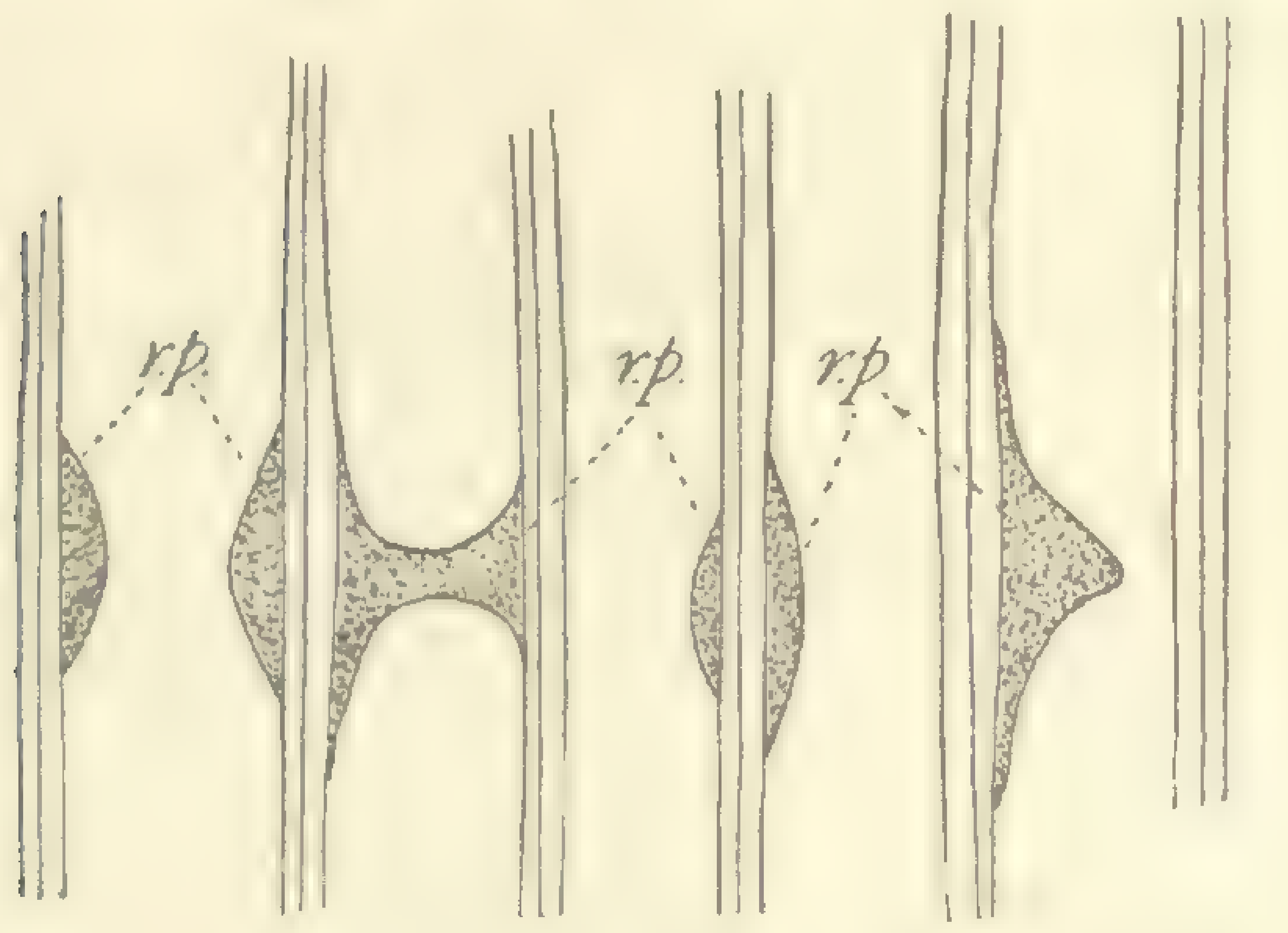

FIG. 34.— *Agathis australis.* Radial section showing the origin of the resin plates (*r. p.*). × 225.

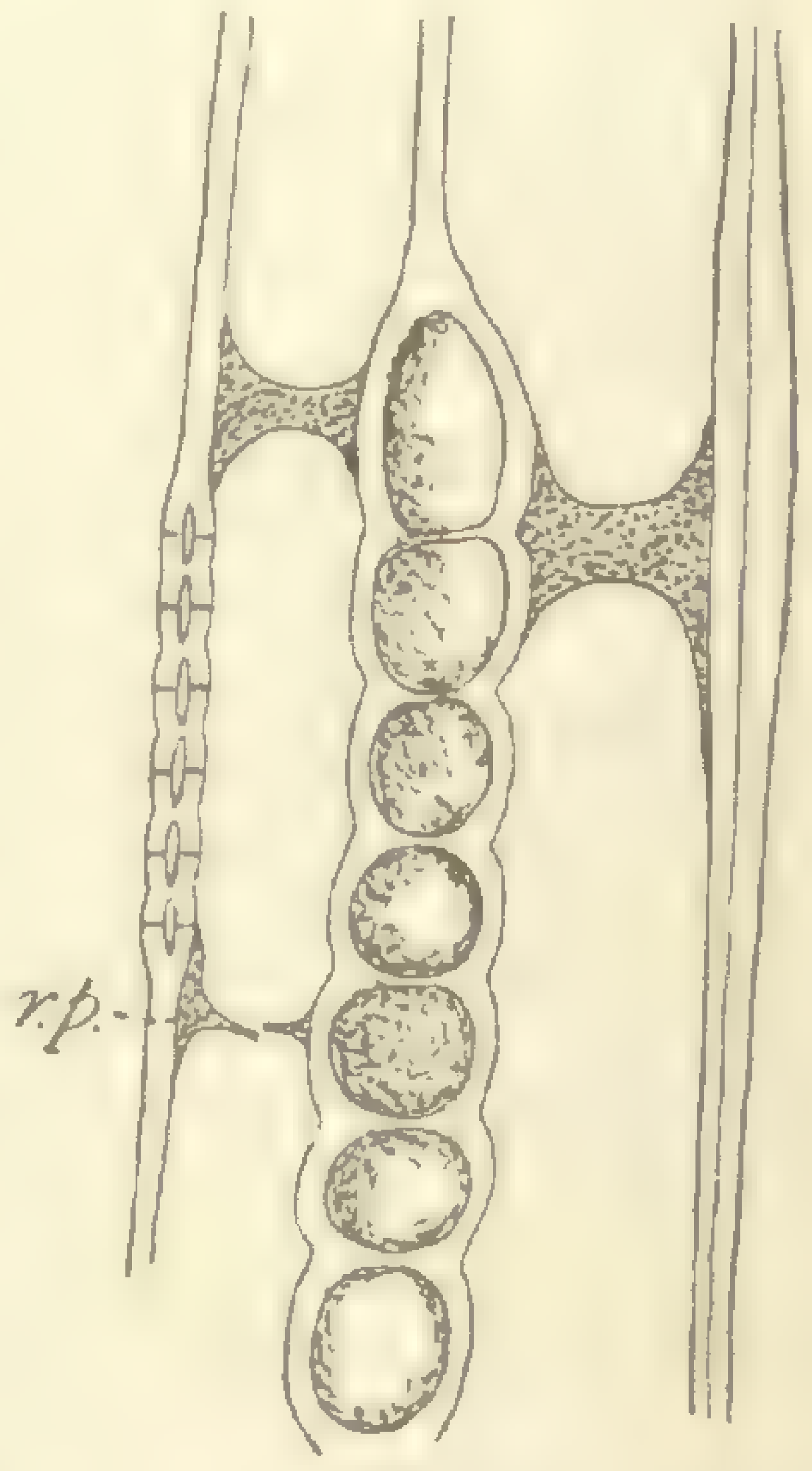

FIG. 35.— *Agathis australis.* Tangential section showing the relation of the resin plates and the medullary ray, and a fractured plate (*r. p.*). × 225.

the ruptures which they not infrequently exhibit (Fig. 35), and in the various developmental stages which may be seen not infrequently (Fig. 34). These show that resin gathers locally upon the inner face of the tracheid wall, and as its volume increases it projects toward the center from all sides, until complete coalescence occurs.

The facts thus obtained proved most conclusively that the transverse plates are obviously resinous and not of the nature of cellulose, even partially, and the conclusion appeared to be justified that they consist of gum dammar, but of a highly modified and highly refractory character. The same evidence also conclusively shows that the cells in which the plates are developed are normal wood tracheids and not wood parenchyma, which is altogether unknown in both Araucaria and Agathis, within the limits of the investigated species.

We are naturally led to ask what is the purpose of these resin plates? The peculiar form in which the resin is deposited, and the particular location of the plates, points with much force to their connection with some functional activity, since if it were simply a question of storage of the secreted products the latter would hardly be disposed as found but rather after the manner common to so many of the Cupressineæ; and this suggestion gains strength from the fact that both in the particular form of the resin masses and their location in the tissue, Araucaria and Agathis are peculiar among all allied genera. No exact comparison can be established with other plants, and it is difficult to suggest an explanation which is adequate. One thing does seem clear, however, and that is that since these plates are of an impervious nature and developed, in some cases at least, in connection with a special constriction of the tracheid cavity, they offer, and possibly they are specially designed to afford, a definite obstruction to circulation in a vertical direction. In this sense they may be designed to serve the same general purpose that is accomplished by the development of thyloses in the vessels of the angiosperms, or in the resin canals of the higher Coniferæ. It is therefore possible that they may be connected in some way not at present clear, with a more complete restriction of the circulation to a radial direction, and

particularly through the medium of the medullary rays as specialized channels for that purpose.

The occurrence of such resinous tracheids is almost exclusively confined to Araucaria and Agathis, in which it is a feature of particular species, but it is a noteworthy fact that similar structures occur, though rarely, among the higher Coniferæ. In the genus Abies they are prominent features in both *A. fraseri* and *A. grandis*. In the former a transverse section shows them to be prominent and scattering through the summer wood, more rarely in the spring wood, while in the radial section the resin is seen to be massive in the summer wood, forming a peripheral layer in the spring wood. In *A. grandis* the resin is usually more abundant, but otherwise the features are the same.

The taxonomic value of the resin tracheids applies exclusively to Agathis and Araucaria, where they are of specific value, and permits of the differentiation of at least one species in each genus. In Abies such tracheids are so sporadic and present so little constancy as to be of no great value.

Returning to a consideration of the resin cells, these structures are found to be entirely wanting in those species of Taxus (4) and Torreya (3) which are included in the present studies. They do occur, however, in Podocarpus where they present the usual structural features, but they are there remarkable for their number and the great abundance of massive resin which they contain. This distribution in the Taxaceæ does not altogether accord with the conclusions of Eichler (11, p. 35) who states that they occur very sparingly in Taxus, but he makes no mention whatever of their presence in Podocarpus where they are much too prominent to escape even the most casual observation.

In the Coniferæ, resin cells are characteristic of all genera except Picea and Pinus, where they are completely replaced by resin passages. They are therefore features in the wood structure of twelve genera, and they are constant characteristics of all their species, with very few exceptions. Such exceptions apply exclusively to the genus Abies, in which four species — *A. fraseri*, *A. lasiocarpa*, *A. veitchi*, and *A. balsamea* — are wholly devoid of such structures.

The recognition of the resin cells presents no difficulty in the great majority of cases because of the abundance and depth of color of the resinous contents. This finds its most complete expression in Taxodium, Sequoia, Cupressus, etc. In Abies, on the other hand, where these cells have experienced extreme numerical reduction and where there also seems to be a corresponding reduction in their secretory power, it is impossible to recognize them in this way. In such cases it is often possible to distinguish them by their slightly different form and somewhat thinner walls as compared with the adjacent wood tracheids; by their situation slightly in advance of the outermost row of summer wood tracheids; and most particularly by their pitted terminal walls when the latter lie near the plane of section. This last feature may also be relied upon in all other cases when any element of doubt is involved (Fig. 36). In longitudinal section the characteristic form of the cell serves to distinguish

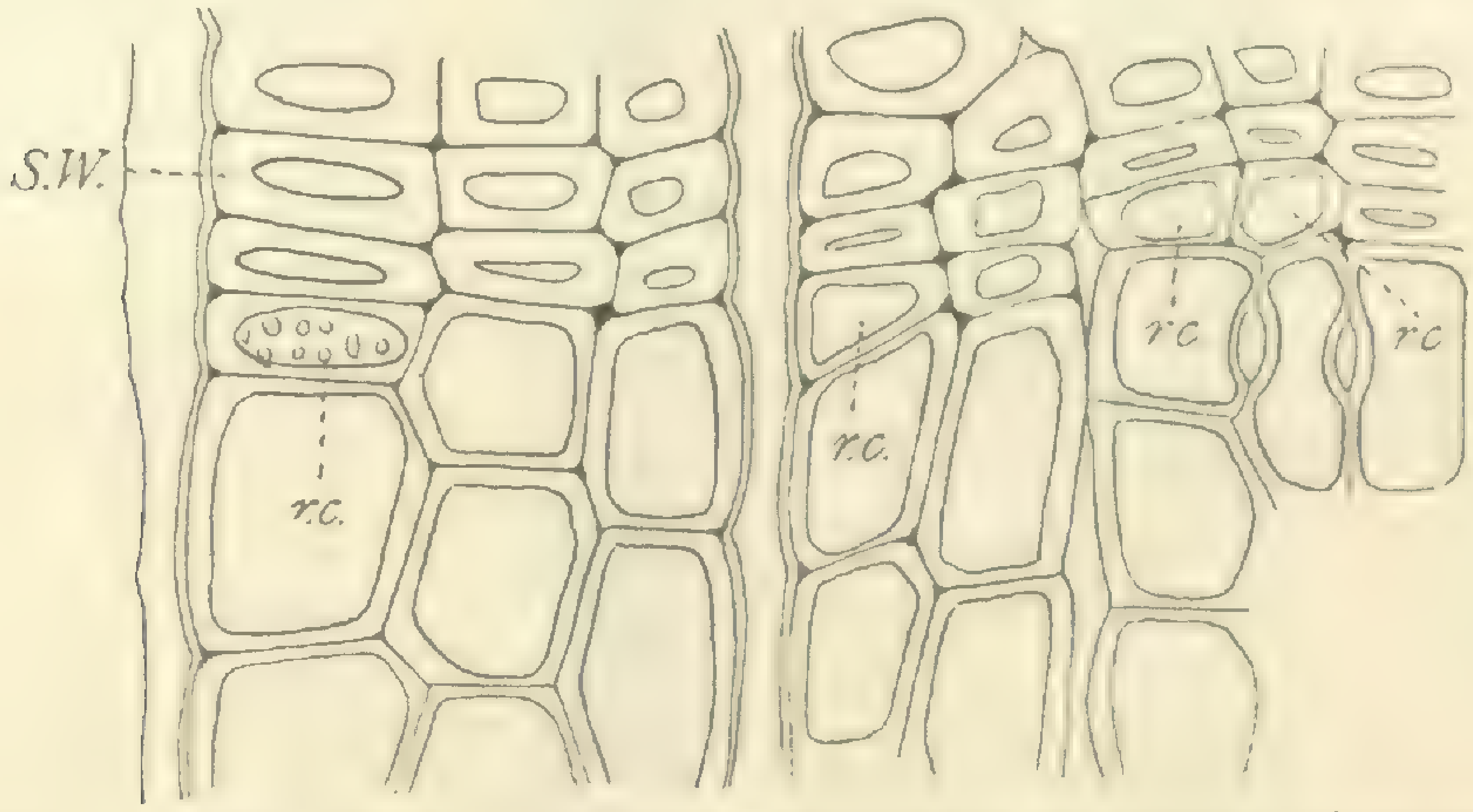

FIG. 36.— *Abies amabilis*. **Transverse section showing the positions and structure of the resin cells (*r. c.*) on the outer face of the summer wood (*S. W.*).** × 300.

it beyond all doubt, even in the absence of resinous contents. Whether exposed in radial or tangential section, the cell has the form of a narrow cylinder upwards of 300 μ in length, and always several times longer than broad, except in cases where there is a definite tendency, through aggregation, to the formation of resin canals.

The resin cells sometimes occur in pairs, but more generally as isolated structures separated by one or more tracheids. The terminal walls are transverse and more or less strongly marked with simple pits. The side walls, especially the radial, are pro-

vided with simple pits, though often few in number, and this feature serves to a large extent, to assist in their differentiation from adjacent tracheids of similar form (Figs. 36 & 38). It nevertheless not infrequently happens that in transitional forms, such as are met with in *Sequoia sempervirens* (Fig. 37*c*), bordered pits occur on the lateral walls.

The resin is in all cases massive and often very abundant.

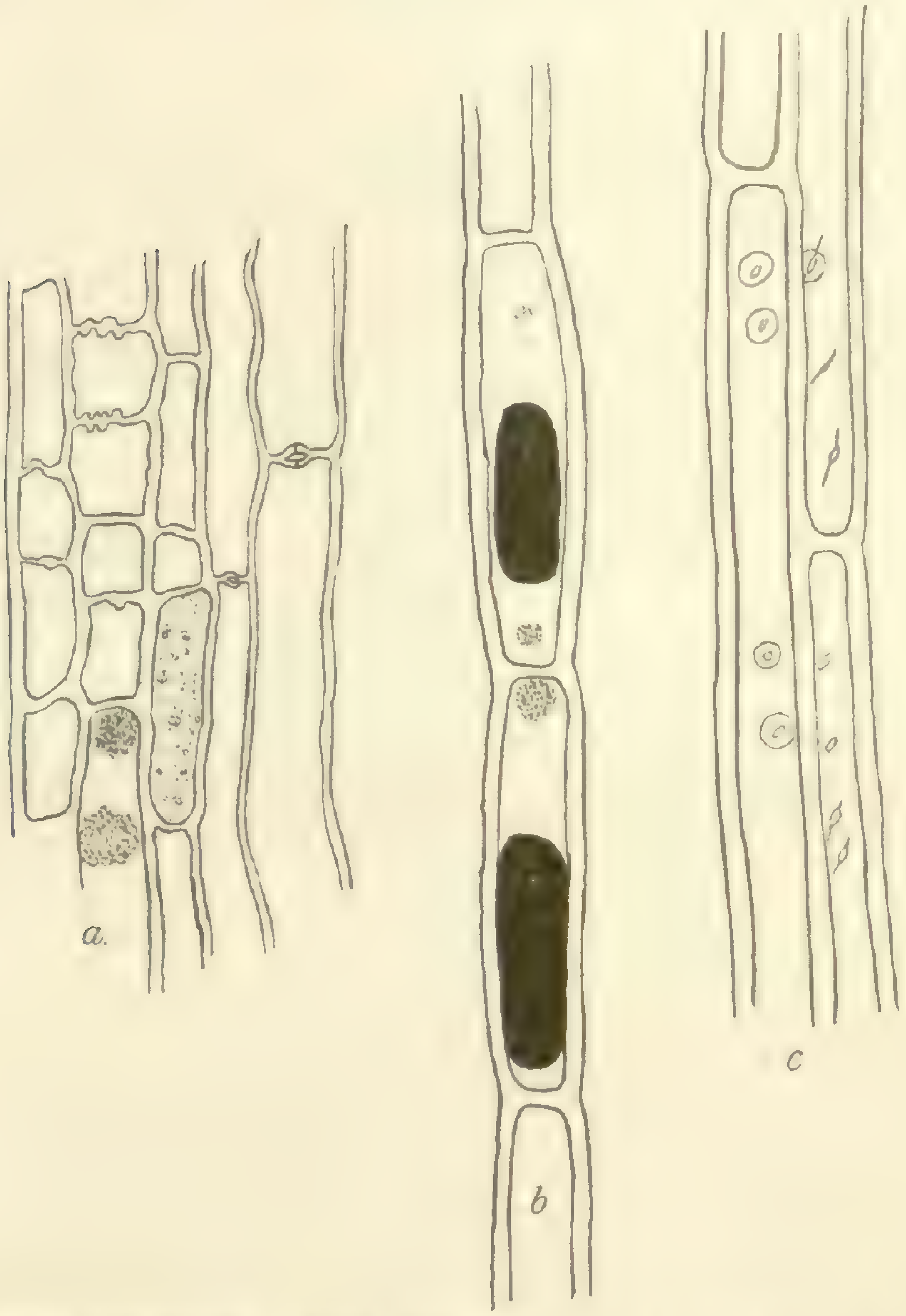

FIG. 37.—*Sequoia sempervirens.* Radial sections showing (*a*) the form of the resin cells and the associated parenchyma tracheids; (*b*) resin cells from the spring wood showing the form of the resin; (*c*) resin cells showing transitional forms with bordered pits. × 200.

In such genera as Taxodium or Sequoia it completely fills the entire cell cavity (Figs. 39 & 40), but in Larix, Tsuga and Pseudotsuga it takes the form of a peripheral layer in immediate contact with the inner face of the cell wall (Fig. 42). The reduction thus indicated is, in some species, carried to such an

extent that the resin is barely recognizable, while in Abies it is wholly wanting.

A relation of more than ordinary interest is to be found in the relation of the resin cells to certain forms of tracheids. In *Sequoia sempervirens* it commonly happens that the resin cells lie in immediate contact with tracheids of special form. These structures are wholly unlike the wood tracheids among which they are found, but they are, in all essential respects, like the tracheids of the medullary rays. They have the form of long, cylindrical elements with abrupt terminations, and they thus bear an external resemblance in form to the wood parenchyma cells with which they are associated. They differ, however, in the distinguishing presence of bordered pits upon their side and terminal walls (Fig. 38*a*). The relations of these two elements is nevertheless a much more intimate one than is implied by mere association. In Sequoia an interchangeable relation is manifested as already pointed out, in the occurrence of resin cells with bordered pits (Fig. 37), while in *Abies amabilis* (Fig. 38) resin cells and tracheids also form a coterminous series. It is thus obvious that we have here precisely the same interchangeable relations that have been found to occur in the medullary rays, and it is evident the one element must arise through modification of the other. The precise order of this sequence is not altogether clear from the available data, but the fact that ray tracheids are derived from their associated parenchyma cells, and that in such types as Podocarpus, Taxodium, etc., the resin cells occur without tracheids, while the latter do occur in Sequoia and especially in Abies, seem to justify the inference that here also they are derived forms, having their origin substantially in special modifications of the parenchyma elements. In view of these relations, it is necessary to distin-

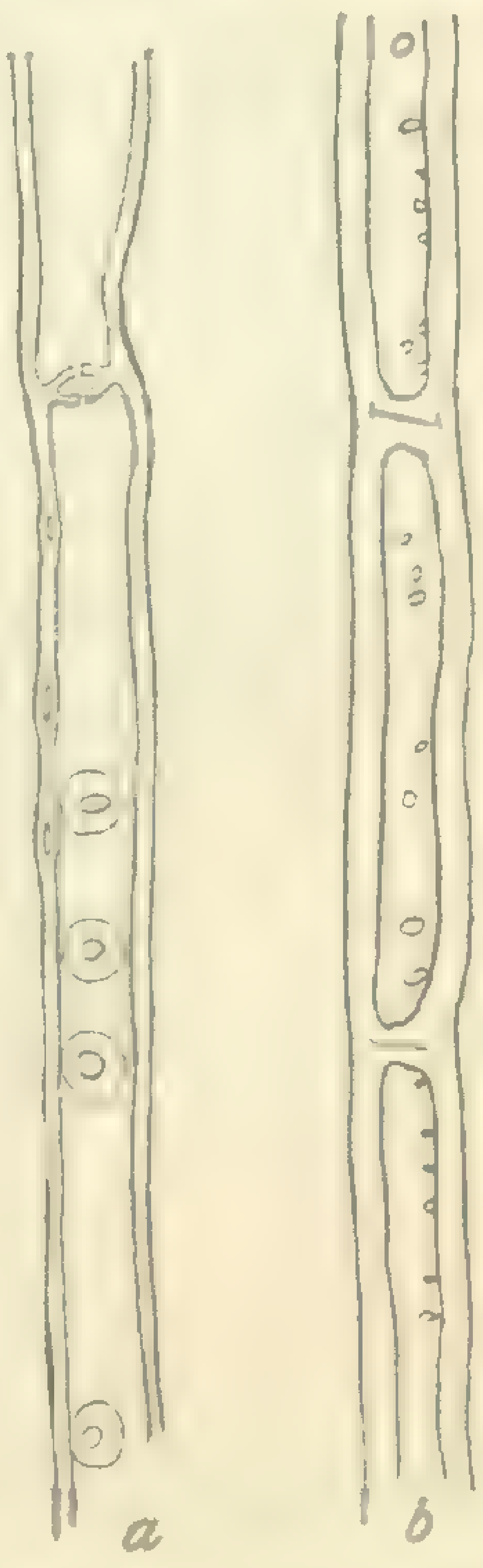

FIG. 38. — *Abies amabilis.* Radial section showing (*a*) the structure of the parenchyma tracheids; (*b*) the structure of the resin cells: *a* and *b* being normally coterminous. × 200.

guish such elements as *parenchyma tracheids* in order to establish their proper identity and differentiate them from the wood tracheids, which have a wholly different origin, as well as from the ray tracheids, which have a wholly different location. It is probable that the parenchyma tracheids also serve a similar purpose to the ray tracheids with respect to the distribution of nutrient fluids. The origin of the parenchyma tracheids as suggested finds support in the statement of Eichler (11) that the wood parenchyma arises through the activity of the cambium cells, abundantly in the Cupressineæ and Abietineæ, forming in exceptional cases the epithelium of the resin canals, since it at the same time shows how the parenchyma tracheids arise and how they may be intimately connected with the wood-parenchyma; but it finds additional support in a knowledge of the genesis and structure of the resin passage.

In Sequoia and Abies we have two genera which are remarkable for their transitional forms of structure, affording a fairly clear conception of the genesis of the resin passage. In each case there is a well defined tendency toward the aggregation of the resin cells into compact groups which take the form of longitudinal strands, enclosed on all sides by the accompanying parenchyma tracheids. Under such circumstances the individual cells undergo a continual reduction in length until they eventually become but two or three times longer than broad, or they may even become isodiametric. This change is not accompanied by any alteration in the thickness of the walls in the earlier stages of development, but as a result of such a shortening the effect is to bring about the concentration of a greater number of simple pits within a given area. Such cells, therefore, are always more strongly pitted than those which are isolated and of greater length. When aggregates of this sort have attained to a certain degree of development a line of cleavage arises in the center of the mass and results in the formation of an intercellular space which, according to Eichler (11), always arises schizogenously. This space is short and either isodiametric or but little longer than broad, the length coinciding with the principal axis of growth. Such cyst-like reservoirs or sacs represent the primitive form of the resin canal, and they

are typically developed in Sequoia, Abies and Tsuga. They always form a continuous series extending in a direction parallel with the axis of growth; but as the type of reorganization advances they merge, forming a continuous canal such as may be found typically in Pseudotsuga or Pinus. From these statements, then, it is clear that the parenchymatous resin cells undergo modification in two directions, passing into parenchyma tracheids, on the one hand, and on the other becoming shorter

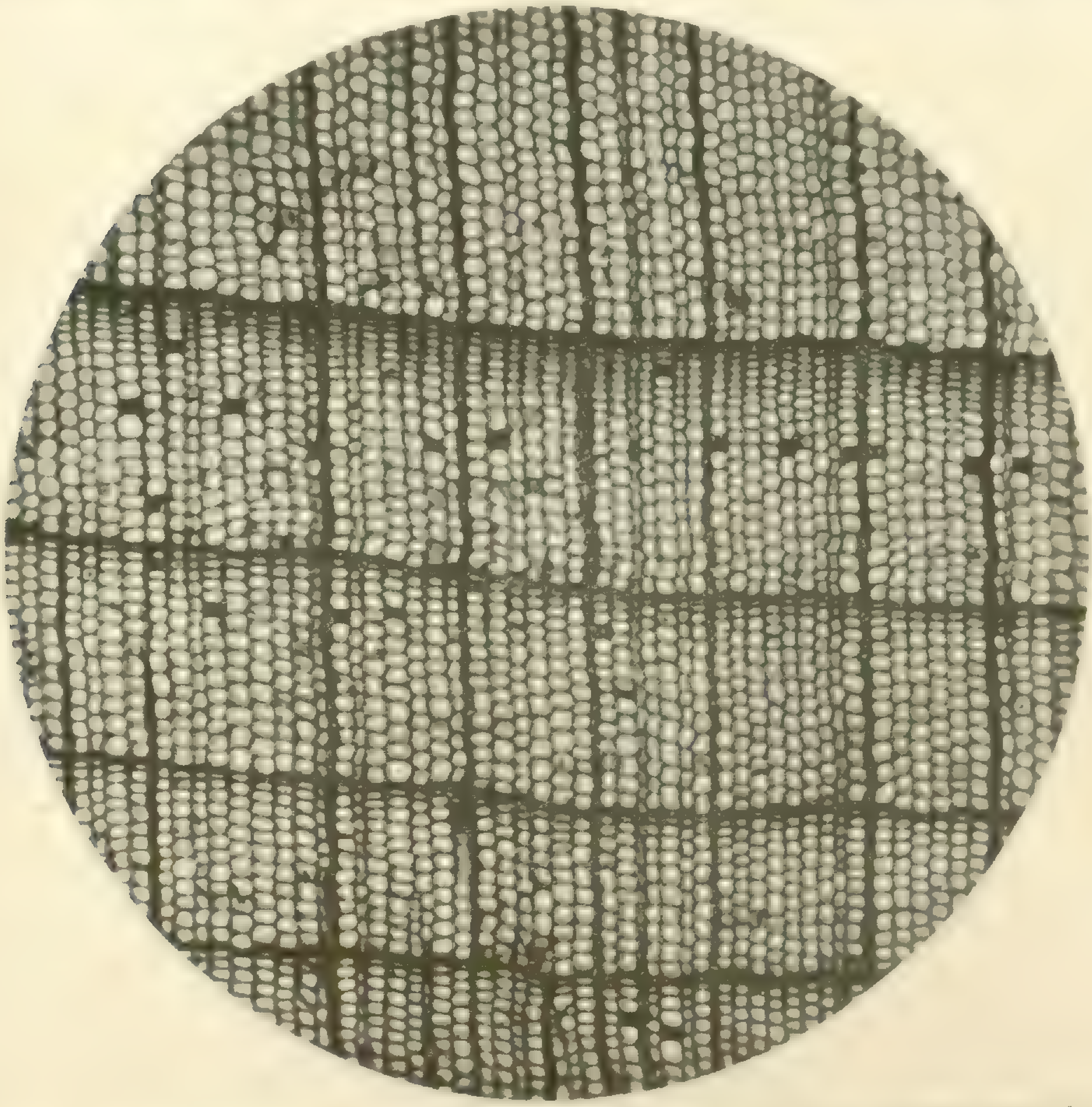

FIG. 39.—*Thuya dolabrata.* Transverse section showing the scattering distribution of the resin cells. × 55.

and shorter, according to conditions of aggregation, until they pass into short cells which eventually constitute the epithelium structure of the somewhat complicated resin passage, the latter thereby becoming the expression of a peculiar aggregation of resin cells. Whatever the stage of development may be, the resin passage is always found to be composed of structural elements arranged in the following order from without toward the center: (1) parenchyma tracheids, (2) resin cells eventually

forming an epithelium and (3) the central reservoir in the form of a cyst or canal. This structure is fully exemplified in the genus Pinus, where the highest form of development is attained.

While the occurrence of resin cells in particular genera is a feature of great taxonomic value, their importance in this respect is greatly emphasized by the particular form of their distribution and the constant tendency they exhibit toward the formation of definite aggregates. In Thujopsis and Cryptomeria (Fig. 39)

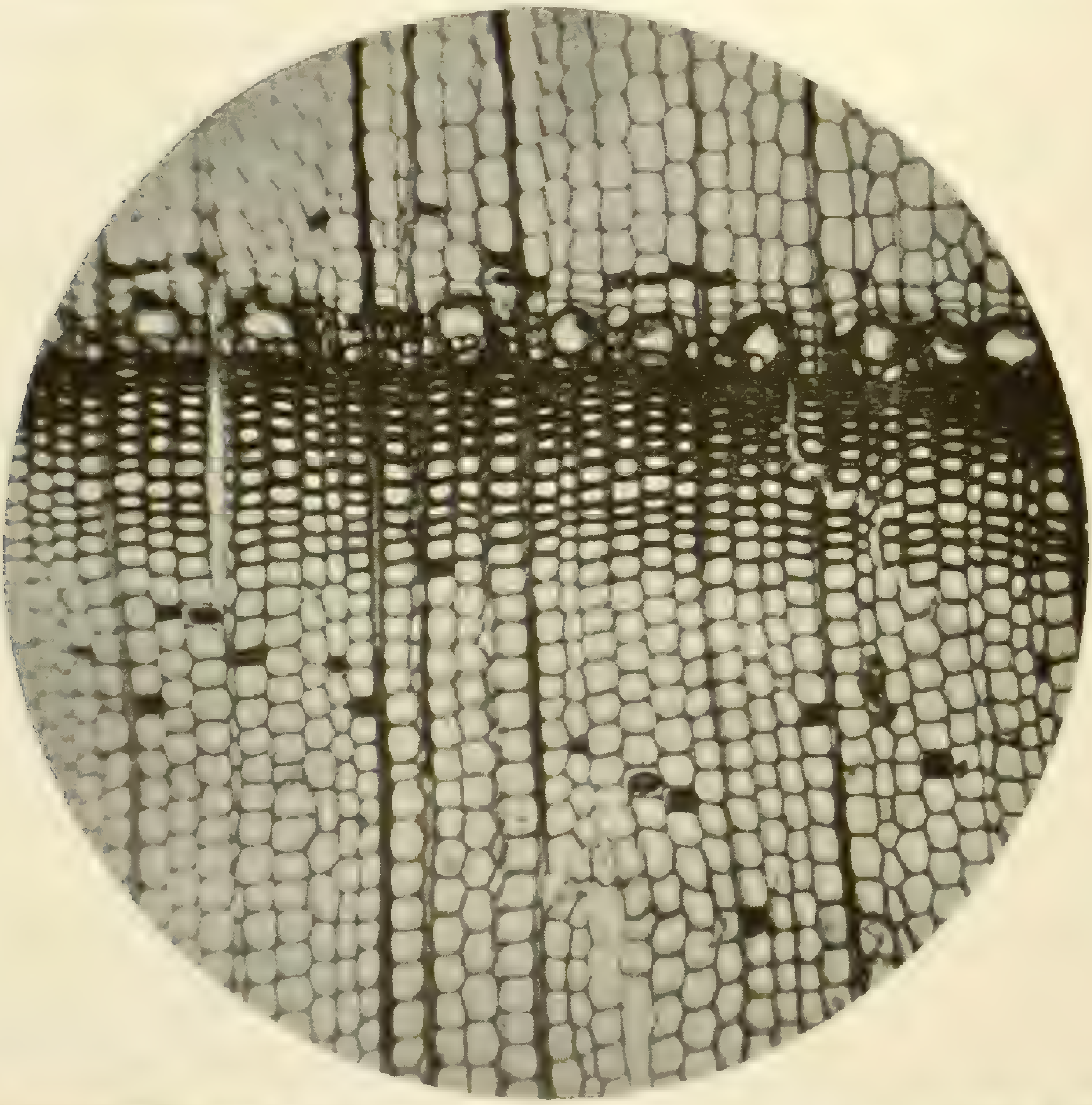

FIG. 40.—*Sequoia sempervirens.* Transverse section showing scattering resin cells in the spring wood, and contiguous resin cysts with aggregates of resin cells on the outer face of a growth ring. × 55.

the resin cells are always scattered throughout the entire transverse section and they show no tendency to the formation of aggregates. In Podocarpus, where there is a notable increase in numbers, the same general law of segregation prevails, but there is nevertheless a somewhat well defined tendency toward aggregation. In Thuya 66.6% of the species show definitely scattering cells, 33.3% show the cells to be scattering with a

tendency toward a more compact disposition, while in 33.3 % the cells fall into well defined aggregates or an approximation to such an arrangement. The genus Sequoia is characterized chiefly by the widely scattering distribution of the resin cells (Fig. 40), but in *S. sempervirens* there are individual cases in which there is also a definite aggregation into groups. In Cupressus 53.9 % of the species are distinguished by the presence of widely scattering cells which become definitely arranged in

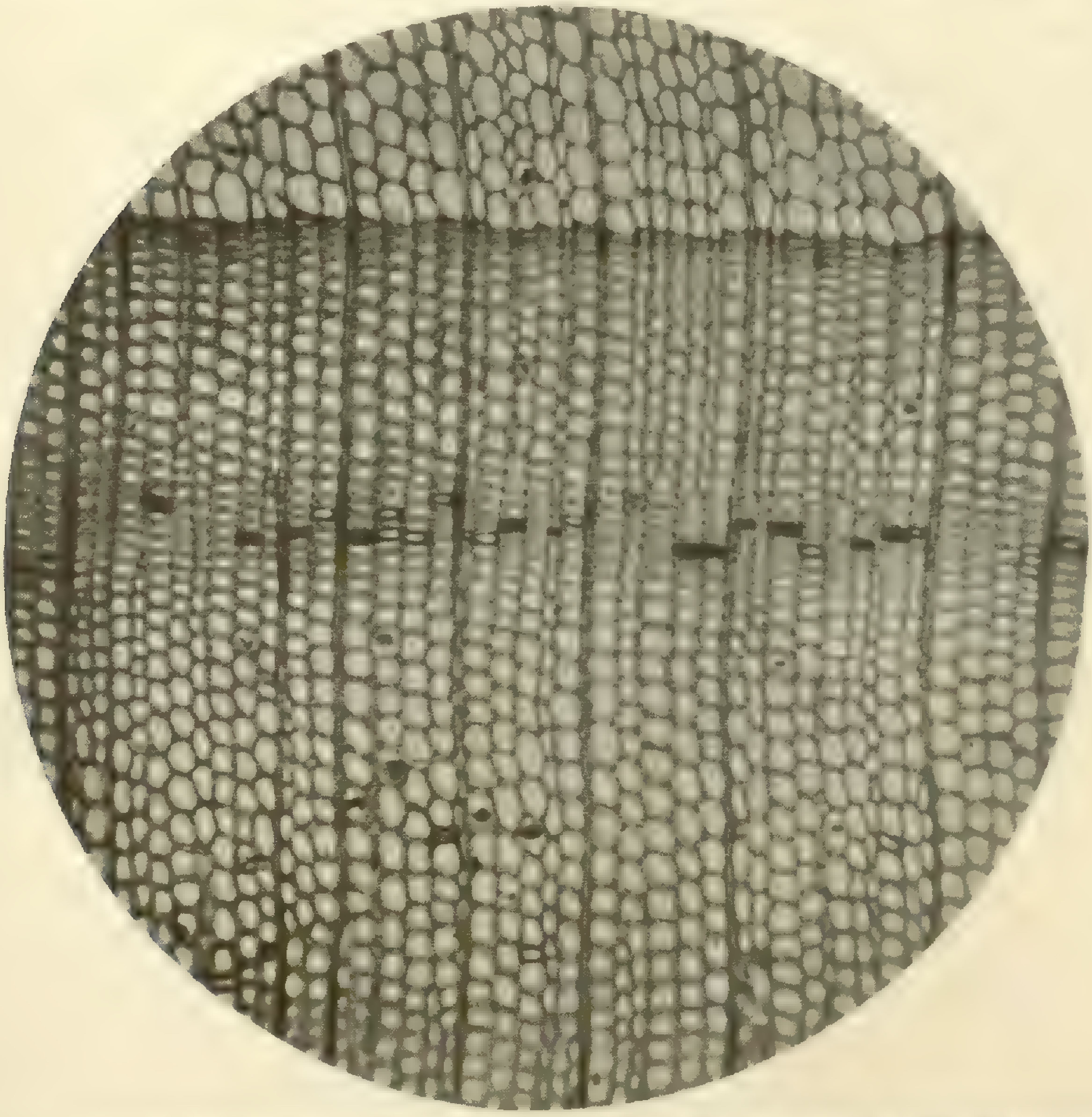

Fig. 41.—*Taxodium distichum.* Transverse section showing the resin cells forming a definite zone. × 55.

zones in 38.4 %, and aggregated into groups in 7.7 % of the species. It will be observed here that this feature of distribution is, on the whole, more pronounced in the relatively primitive genera, and that it diminishes in force in the genera of a relatively high order.

In Taxodium (Fig. 41) and Libocedrus, both of which are distinguished by the presence of very prominent resin cells, these structures are disposed in well defined zones which are concen-

tric with the growth rings and lie either in the spring or summer wood, or in both. This is to be interpreted as a definite tendency to aggregation which is nevertheless not fully expressed, since in each case there are numbers of cells which are not zonal in their distribution, but which conform to the law applicable to Thujopsis and Podocarpus. In Juniperus the cells are typically zonate, being also scattering in only one species. In Abies only 63.6 % of the species bear resin cells. These are

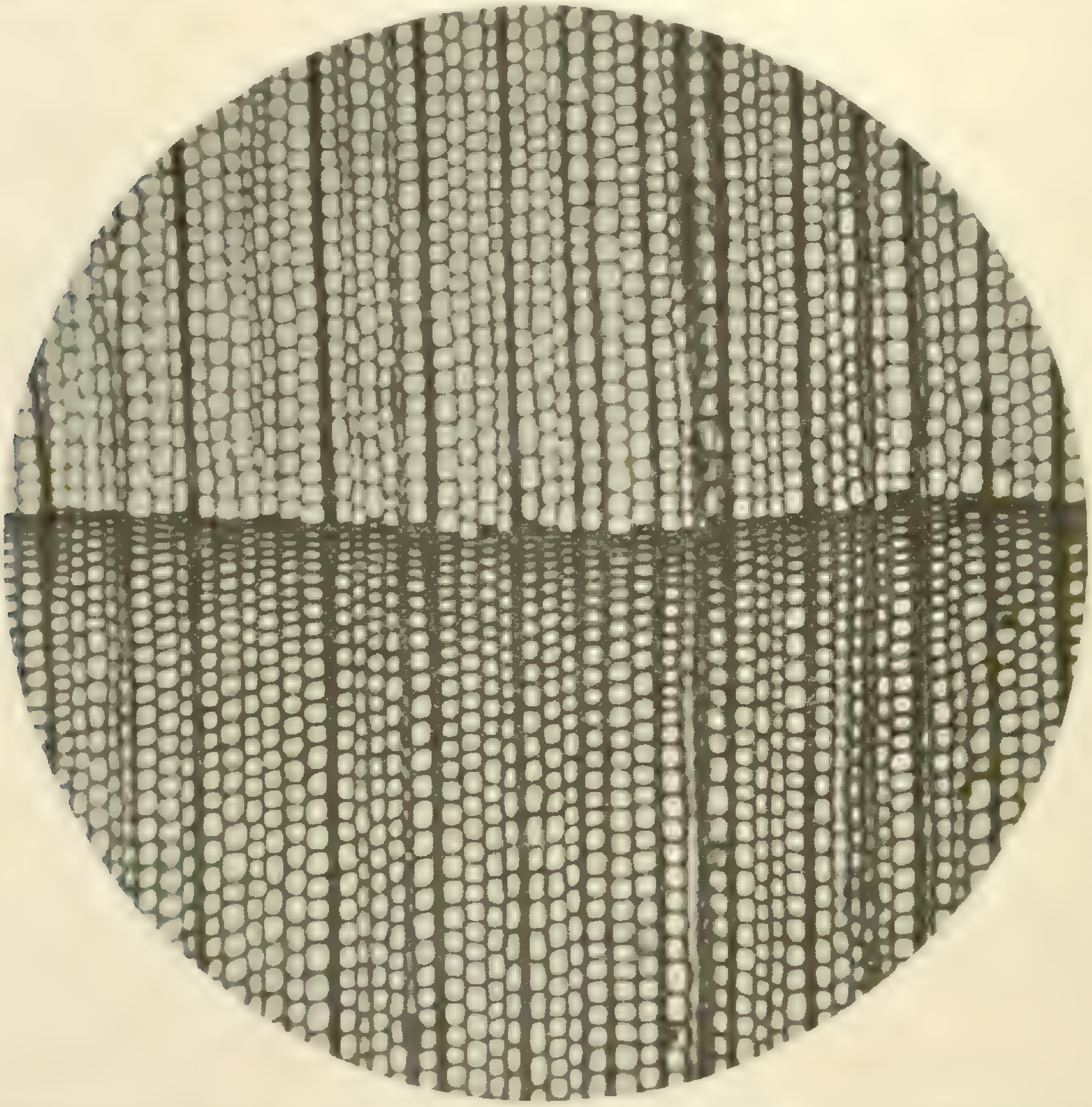

Fig. 42.— *Tsuga pattoniana.* Transverse section showing the distribution of the resin cells on the outer face of the summer wood. × 55.

neither scattering nor zonate in the sense of the previous types, but it is to be observed that in 50 % of such cases, or in 36.3 % of all species, they are aggregated in groups as a preliminary step to the formation of resin passages. On the other hand, 36.3 % of all species show the resin cells to be few, inconspicuous, non-resinous and scattered along the outer face of the summer wood. This, for reasons which will appear more fully later, is to be regarded as a phase in distribution leading to the final

obliteration of such structures, which is fully accomplished in 36.4 % of all the species as represented by *A. balsamea*, *A. fraseri*, *A. lasiocarpa*, *A. veitchi*. This last form of distribution is wholly typical of Tsuga (Fig. 42), in which there are no other resin cells than those on the outer face of the summer wood. Finally, in Picea and Pinus, there are no separate resin cells in any of the situations described, since they have been completely replaced by highly organized resin passages. It thus appears that the distribution of the resin cells presents four variants which bear a direct relation to the organization of resin passages, as the latter eventually replace the former. These facts will appear somewhat more clear from the following summary :

TABLE SHOWING PERCENTAGE DISTRIBUTION OF RESIN CELLS.

	No. of species.	% of occurrence.	Scattering.	In zones.	Grouped.	On the outer face of summer wood.
Ginkgo . . .	1	000.00				
Agathis. . .	1	000.00				
Araucaria . .	3	000.00				
Torreya . .	3	000.00				
Taxus . . .	4	000.00				
Thujopsis . .	1	100.00	100.00			
Cryptomeria. .	1	100.00	100.00			
Podocarpus .	1	100.00	100.00	(100.00)		
Thuya . . .	2		66.60			
	1 = 3	100.00		33.30		
	1		(33.30)			
Sequoia . .	2 = 2	100.00	100.00			
	1				50.00	
Cupressus . .	7		53.90			
	5 = 9	100.00		38.40		
	1				7.70	
Taxodium . .	1	100.00	(100.00)	100.00		
Libocedrus .	1	100.00	(100.00)	100.00		
Juniperus . .	11 = 11	100.00		100.00		
	1		1.10			
Abies . . .	4 = 7	100.00				36.30
	5				45.50	
Tsuga . . .	2 = 5	100.00			33.30	
	5					100.00
Pseudotsuga .	2	100.00				100.00
Larix . . .	4	100.00				100.00
Picea . . .	10	000.00				
Pinus . . .	41	000.00				

Figures in parentheses refer to exceptional forms of occurrence.

From such data it is clear that the distribution of the resin cells bears an important relation to the recognition of sub-generic groups and even of species. But viewing these structures from the broader standpoint of the Coniferales as a whole, it is obvious that they must be placed among the structural elements which belong to the first rank for taxonomic purposes.

We are now in a position to determine what relation, if any, such resin bearing elements bear to questions of phylogeny, and we may first of all consider the resinous tracheids. These structures have been seen to be peculiar to Agathis, Araucaria, and Abies, in which they occur only in certain species. In answering this question, we cannot avail ourselves of evidence derived from fossil plants, since it is in such cases of a negative character. Neither Cordaites nor Araucarioxylon affords definite proof of the presence or absence of such structures, since they do not appear in any of the published diagnoses, and our own studies have not resulted in their recognition. If originally present, they must have been obliterated in the course of fossilization. We must therefore depend entirely upon such evidence as is afforded by existing species. From this point of view it is obvious that they furnish no evidence as to the origin of either of the three genera in which they occur. It is, on the other hand, possible to determine from other data, that both Agathis and Araucaria are much inferior to Abies in point of structural organization and development, and from this we may be permitted to conclude that the resin tracheids of Abies are vestigial forms of elements which were typically developed in Agathis and Araucaria, and possibly characteristic also, of their progenitors. If such inferences are to be regarded as justifiable, they go far to support the idea of a common origin for all three genera, and they thus lend force to conclusions which lead to the same result, but upon the basis of independent data.

From a study of the distribution of the resin cells, it is apparent that they fall into four categories in which the typically segregated cells may be held to represent the most primitive form of disposition. This view is greatly strengthened by the observation that in all such cases, the resin cells are rarely if at all accompanied by parenchyma tracheids, while the structure of

the cell is farthest removed from that which is found to enter into the composition of resin passages, whence they are also to be regarded as of a primitive character. This view is supported by the observed fact that those genera and species in which such segregations occur, are also of a relatively primitive type. With an advance in organization, there is a tendency to the formation of aggregates as expressed in the zonal distribution of Taxodium, Libocedrus or Sequoia, where we also find the definite formation of groups of cells which later exhibit the initial stages in the formation of a definite canal. But in Sequoia, as also in Abies where similar changes take place, the more complete aggregation of the cells is invariably accompanied by structural alterations whereby they become greatly shortened and more strongly pitted, while they are always accompanied by parenchyma tracheids with which they are interchangeable. In this connection it is also to be noted that the aggregates in Sequoia, Abies and Larix leading to the formation of resin sacs, are always disposed in a zonal manner, conformably to the zonal disposition of the separate elements, a relation which is in direct harmony with the view already advanced, that the zonal disposition of the isolated cells is an advance upon the strictly segregated form, and that it leads directly to the formation of resin passages. Following upon the zonal distribution, a more complete aggregation results in the formation of local groups of short, resin cells ultimately leading to the formation of a true resin canal. Such a feature of distribution, occurring in genera which, from other data, may be shown to be relatively high in development, is in itself significant; but we further find that the scattering, zonal and grouped forms bear such relations to one another, that the real succession is in the order already given. Thus while both species of Sequoia are characterized by scattering cells, *S. sempervirens* also shows them aggregated to form groups and eventually imperfectly organized resin canals. Or in Cupressus, the transition is expressed in a more complete form, involving all three modes of distribution. In Tsuga there is an obvious tendency toward the elimination of the resin cells which are now greatly reduced in numbers and confined to the outer face of the summer wood. In Abies a similar tendency is also manifested,

but it is expressed in a different way, and just here we must note a fact of more than ordinary significance. Resin cells are present on the outer face of the summer wood in *A. grandis*, *A. concolor*, *A. amabilis* and *A. magnifica*. Groups of resin cells are present in *A. nobilis*, *A. concolor*, *A. bracteata* and *A. firma*, but it will be seen that in only one case — *A. concolor* — are the two forms of distribution presented in the same species. This is in direct conformity with the idea that the resin passage eventually displaces the resin cell, bringing about an obliteration of the latter, and it goes far to support the idea that with respect to these particular structures, the genus Abies occupies a transitional position, standing next to Picea and Pinus, from both of which the resin cells have completely disappeared. Furthermore, from another point of view, the gradual replacement of the resin cells appears to be indicated by a corresponding reduction in the contained resin. Nowhere is the resin so abundant in the resin cells, as in those genera like Podocarpus and Taxodium, which show no development of resin passages, even in their most simple forms; but with the development of resin sacs, as in Abies or Sequoia, or of resin passages as in Larix and Pseudotsuga, there is a remarkable diminution of the resin, apparently in direct response to its more ready production by more specialized structures.

The genus Abies then, appears to form a transition group, having parallelisms with Agathis and Araucaria through the occurrence of resinous tracheids; with Thuya, Cupressus, etc., through the survival of isolated resin cells approaching obliteration; with Tsuga, Larix and Pseudotsuga through the development of rudimentary resin canals leading to the formation of definite resin passages; and with Sequoia through the survival of isolated resin cells and the development of rudimentary resin canals. Through these parallelisms the connection appears to be most direct on the one hand with Sequoia, and on the other with Tsuga. This relation of Sequoia to Abies has been shown by Penhallow on former occasions (38), and has more recently been indicated in other ways by Jeffreys (24), but so far as the present evidence is of value, it would not permit us to infer that Sequoia, Abies and Tsuga form a continuous and coterminous

series in the order given, but rather that they represent separate, though short, side lines of development, between which the general sequence is manifested.

Resin Passages.

Structural.

Our studies of the resin cell have shown how peculiar aggregates of these structures lead in a natural way to the organization of resin passages, the structure of which it is now necessary to discuss somewhat in detail, and in doing so it will be most profitable to have reference to (1) the primitive form, (2) the intermediate form and (3) to the advanced or fully organized form.

The primitive form of the resin passage is to be found in Sequoia, Tsuga, and Abies and inasmuch as within these genera they exhibit differences in organization which correspond approximately to the sequence given, it will be necessary to discuss them somewhat in detail, with special reference, however, to Sequoia. This genus possesses special interest with respect to the occurrence and organization of secretory reservoirs, since it is in all probability not only the most ancient genus in which such structures occur, but it is, so far as I am aware, the only genus affording special data with respect to important variations of structure and mode of occurrence. Being also, on the whole, the most primitive of the three genera, I shall deal with it first.

In *Sequoia sempervirens* the secretory reservoirs occur in rows within the initial layers of the spring wood, and they therefore lie exactly on the outer face of the summer wood of the previous year. Within this row the reservoirs are contiguous and in many cases they become confluent so as to form a more or less extended and continuous compound reservoir lying tangentially. In their most rudimentary forms they present the aspect of simple aggregates of resin cells without any differentiation of a resin sac or of an epithelium. In a more advanced stage of development there is produced a central cavity in the form of an intercellular space (Fig. 43, *C*) which has obviously

originated schizogenously. About this the resin cells are generally flattened radially and disposed in such a manner as to suggest the future development of a definite, limiting layer or epithelium. In the completed form of the structure the central space has broadened out and taken a circular form, assuming the character of a definite cyst bounded by as definite a limiting epithelium in which the cells are always flattened radially and disposed concentrically (Fig. 43, *C*). Externally to these cells there may be a second layer of similar resin cells, constituting the outer epithelium, while the whole is enclosed on three sides by a layer of parenchyma tracheids which are exceedingly like

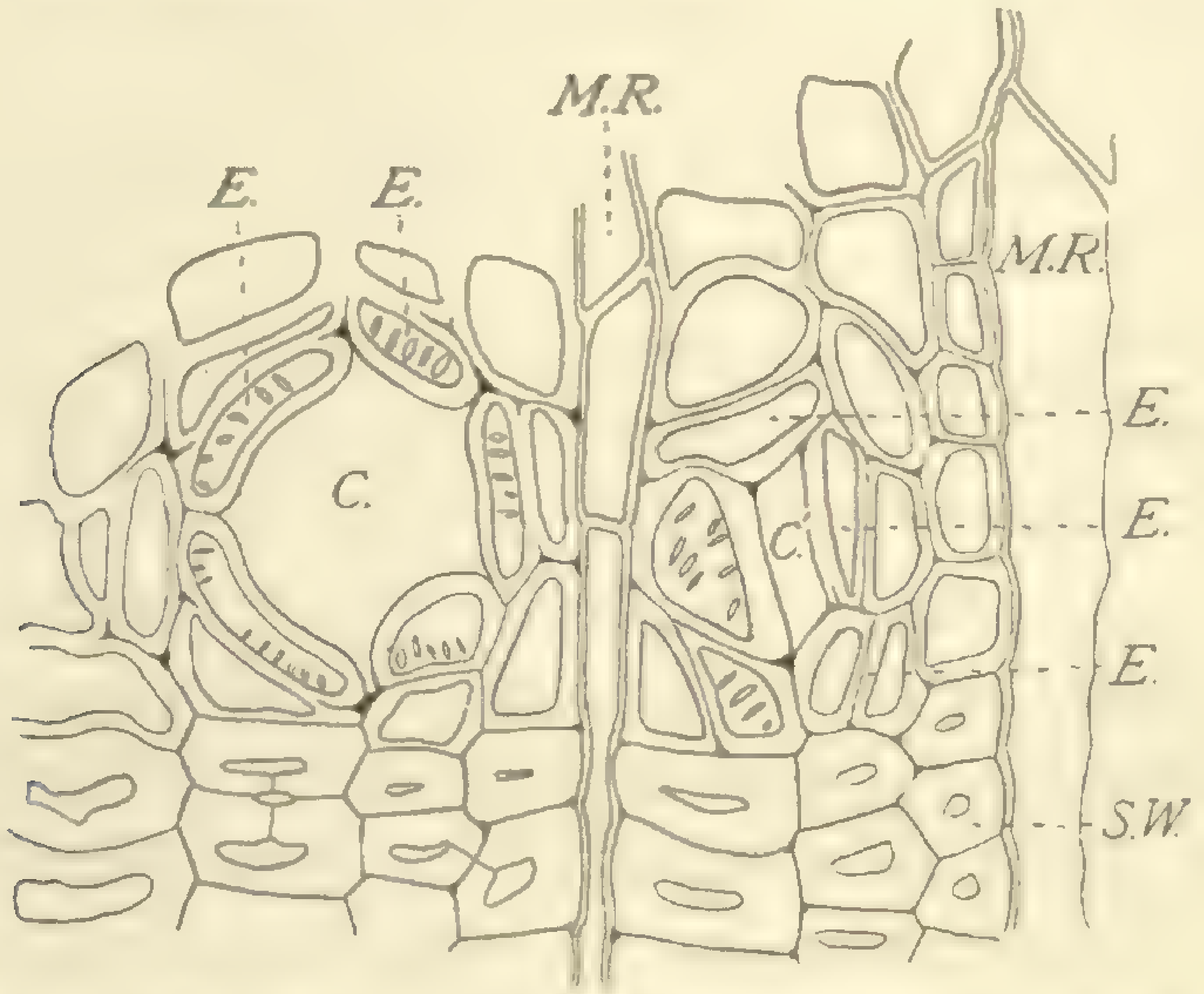

FIG. 43.—*Sequoia sempervirens*. Transverse section showing two contiguous resin cysts, *C*, completed and with a normal epithelium *E*; *C'* an intercellular space as the rudiment of a cyst with imperfectly developed epithelium.' *M. R.* the medullary ray; *S. W.* the summer wood. × 225.

the associated tracheids ot the spring wood, but from which they may usually be distinguished by (1) their greater size and relatively thinner walls, (2) the occurrence of bordered pits on the tangential and terminal, as also upon the radial walls. Such parenchyma tracheids never occur in the adjacent summer wood for very obvious reasons, but on the radially opposite side of the reservoir they are very commonly flattened radially (Fig. 43), and they not infrequently present the same structural aspects as the epithelial cells. The interchangeable relation between resin cell and parenchyma tracheids as already shown would lead us to suspect a substitution in the composition of the epithelium, and

such substitution does actually occur, since it is often to be noted that the second and third rows may be made up, at least in part, of tracheids.

In a longitudinal radial section the reservoir is found to have the form of a sac of varying form and size, but generally elongated parallel with the axis of growth and completely closed at both ends (Fig. 44). The epithelium which immediately defines the limits of the sac generally consists of short, cylindrical cells, while in the second or outer layer the cells become much elongated and several times longer than broad. Beyond this, the third layer consists of parenchyma tracheids readily distinguishable whenever the terminal walls lie near the plane of section, or otherwise as already indicated. Certain deviations from this typical structure require examination. The resin sacs are placed in vertical series of indeterminate extent, but at varying intervals of such a nature that they may sometimes be separated only by a rather thick wall of short resin cells. At other times they are somewhat distant and separated by an extensive vertical tract of resin cells. From this it is obvious that in any given plane of section there will be a great diversity of aspects presented, but in the main exhibiting structural gradations in the development of the reservoir as already recounted. In some cases thick-walled cells of circular outline may be seen

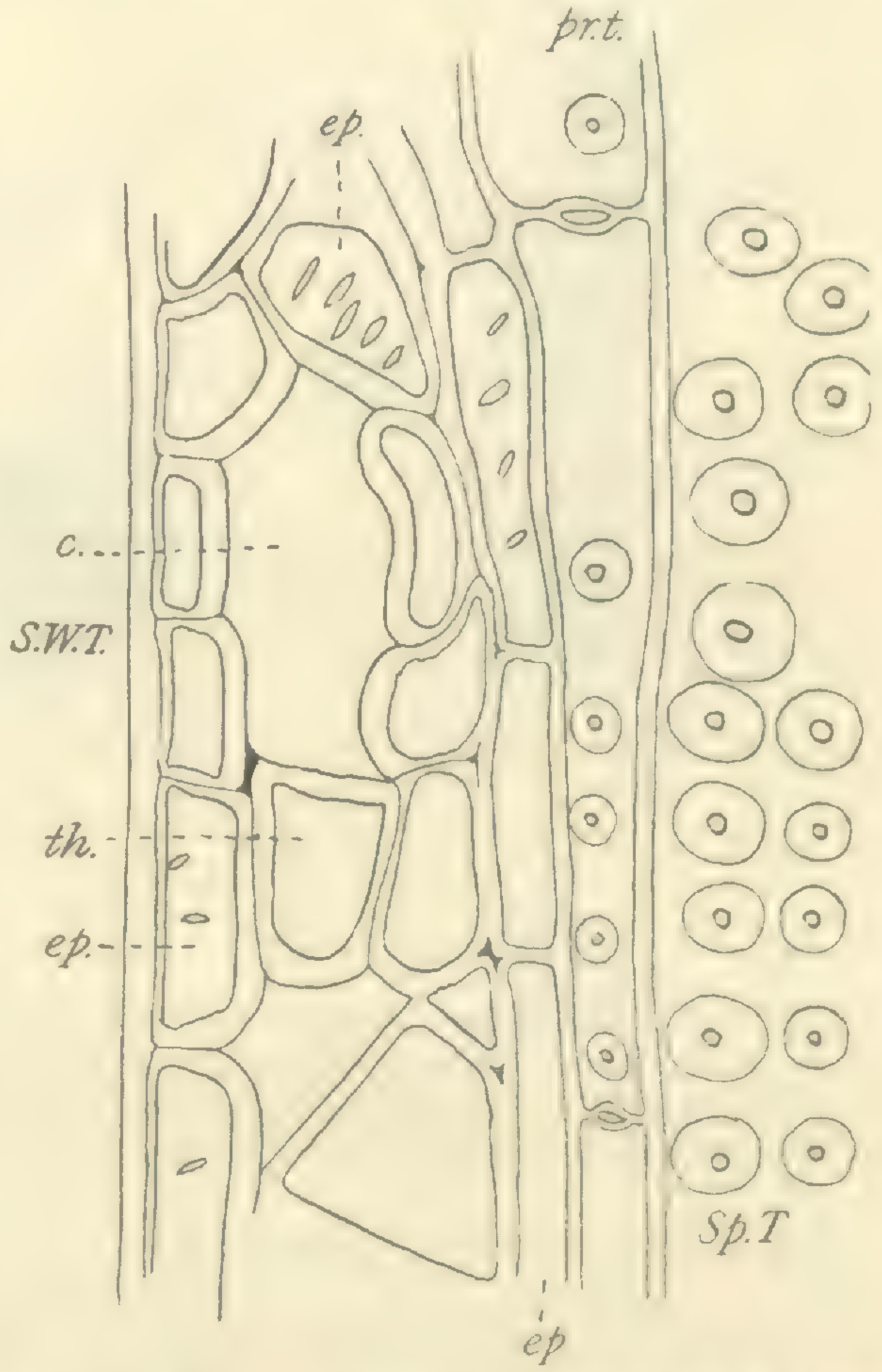

FIG. 44. — *Sequoia sempervirens.* Radial section of a resin cyst, showing the epithelium (*ep.*); the central cyst (*C*) with a thylosis (*th*); parenchyma tracheids (*pr. t.*), and a tracheid of the spring wood (*Sp. T.*). × 300.

in transverse section to stand out from the general line of the epithelium and lie within the cavity proper. More rarely such cells are so multiplied as to fill the entire cavity, and they may themselves be filled with granular resin. Such features are

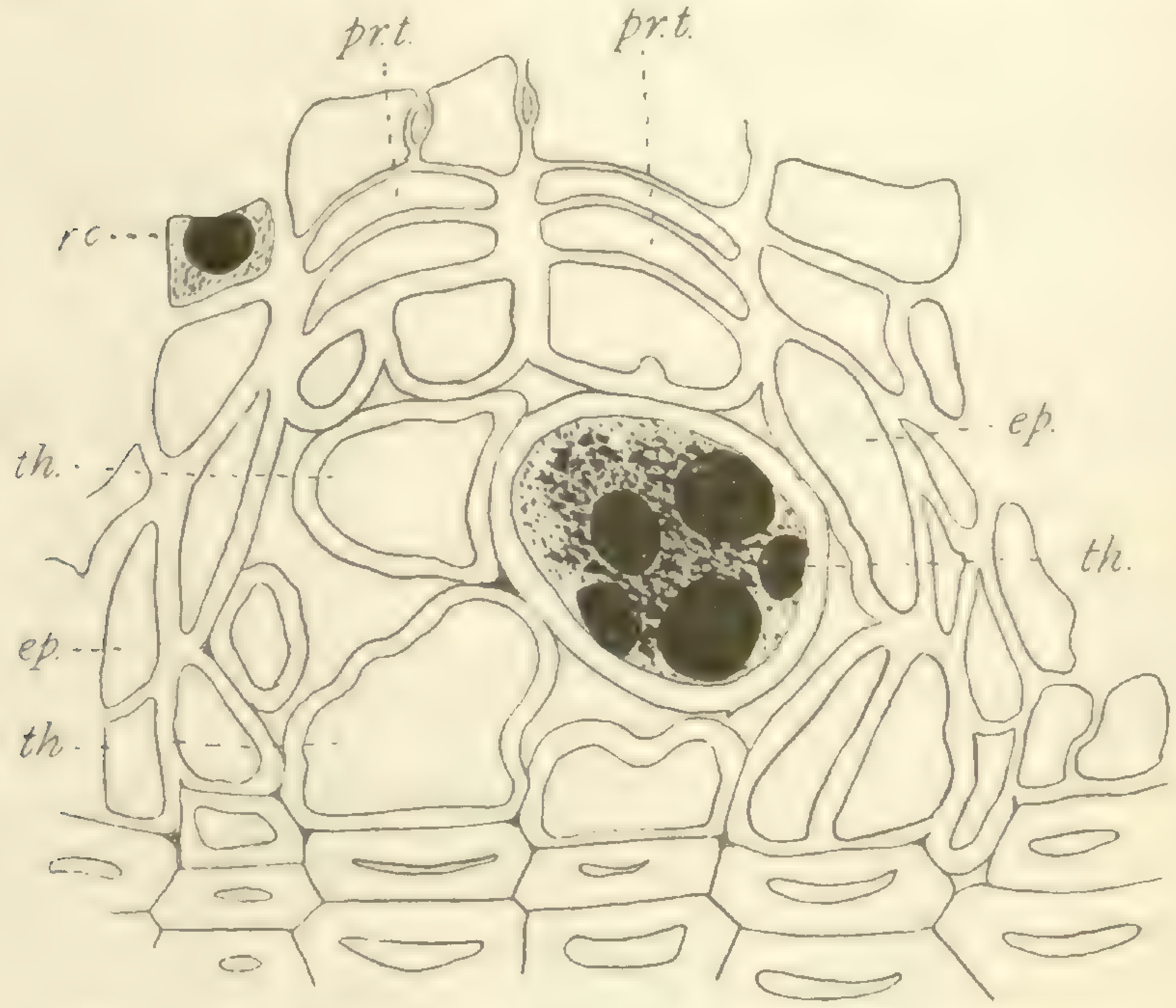

FIG. 45.—*Sequoia sempervirens*. Transverse section of a resin cyst showing an associated resin cell (*r. c.*); the epithelium (*ep.*); the thyloses (*th.*), one of which contains resin, and one of which is directly derived from an epithelium cell; the parenchyma tracheids (*pr. t.*). × 300.

clearly defined (Fig. 45), and it is evident from the way in which such cells originate from the epithelial cells that they are of the nature of thyloses. A longitudinal section through such a reservoir (Fig. 46) shows how such thyloses occupy the entire cavity of the cyst, while in other cases they may be purely local (Fig. 44). Among fossil sequoias similar thyloses form a most characteristic feature in the resin passages of the medullary rays in *S. burgessii*.

In *Tsuga caroliniana* there are no secretory reservoirs, but just in the region between the spring and summer wood of the same growth ring there are peculiar aggregates of resin cells of a more or less rounded outline but forming a continuous series of considerable extent. An analysis of these aggregates shows them to be composed of thick-walled and rounded resin cells, among which there may be a small central intercellular space without any definite organization of epithelium. In such aggre-

gates the component cells are far less resinous than the isolated resin cells of the same section. The parenchyma tracheids are not clearly distinguishable from the associated wood tracheids. In radial section the cells are seen to be very variable, thick-walled and sometimes with more or less prominent intercellular spaces. Between the rays they are several times longer than broad, but opposite the rays they are short, cylindrical and more copiously pitted: while sometimes they may be seen to merge into ray elements and thus to continue their course at right angles to their primary direction. A careful comparison of these cell aggregates with those of Sequoia and Abies leaves little room for doubt as to their structural and functional identity, and we cannot do otherwise than conclude that they represent the most primitive structural condition which is capable of directly giving rise to definite cysts by central cleavage.

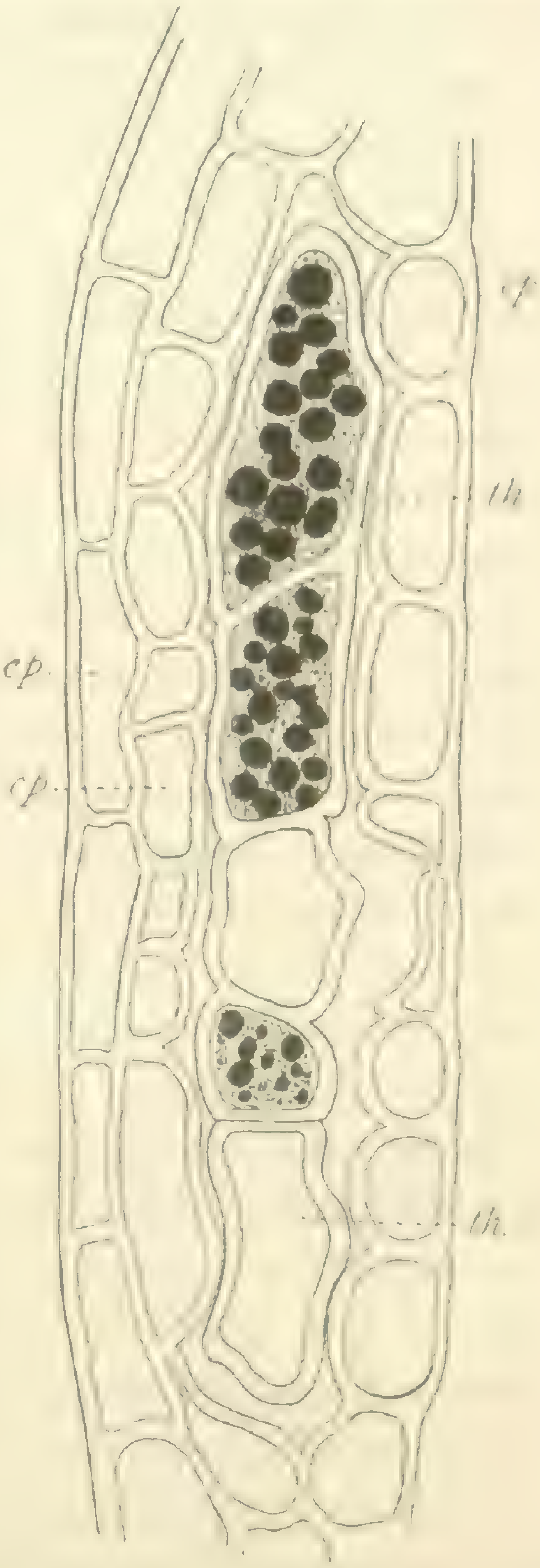

Fig. 46.— *Sequoia sempervirens.* Radial section of a resin cyst showing the epithelium (*ep.*), and the thyloses (*th.*) which completely fill the cyst, and several of which are resinous. This figure corresponds to Fig. 45. × 225.

In *Tsuga mertensisana* the secretory reservoirs are disposed like those of Sequoia, on the outer face of the summer wood, where they form tangential series. They exhibit all the gradations from simple cell aggregates without a central space to perfectly formed cysts with a definite epithelium. This latter is in one, more rarely in two rows, and it is composed of more or less rounded or radially flattened elements. The parenchyma tracheids are few in number, and they are not readily distinguishable from the adjacent wood tracheids. In

longitudinal section the reservoirs are variously rounded or oblong cysts, contiguous or isolated, and forming a longitudinal series. In their general form and structure they are essentially the same as in Sequoia.

In the genus Abies secretory reservoirs occur in at least four species where they form more or less extensive tangential series, within which they are usually contiguous and more or less confluent. They present the same general variations in structural organization as in Tsuga and Sequoia, but in *A. concolor*, and less conspicuously in *A. nobilis*, they are often extended in a radial direction so as to become narrowly oval or oblong, and several times longer than broad. The epithelium consists of a well defined structure composed of one to three rows of cells. The first row, immediately bordering upon the canal, consists of rounded or oval and thick-walled cells which are much smaller than those of Sequoia, and similar to those of Tsuga. They are always characterized by an abundance of strongly defined, simple pits, and many of them contain resin, which usually takes the form of rounded granules of diverse sizes. The parenchyma tracheids are so nearly like the accompanying wood tracheids as, in some cases, to be separable with some difficulty, but they generally surround the resin sac, at least within the limits of the spring wood, and they not infrequently replace the parenchyma cells of the epithelium more or less completely. Not infrequently they form somewhat extended radial series from the epithelium into the spring wood, as in Picea (Fig. 48). In such cases they are usually recognizable by their rather unusual size and thinner walls, and in addition they commonly show bordered pits on the tangential walls. When the terminal wall lies sufficiently near to the plane of section, it shows from one to several rather large bordered pits, and by this feature such tracheids may be located with much certainty. Thyloses have been definitely noted only in the case of *A. concolor*, in which species they are essentially of the same general character as in Sequoia, They are thick-walled and either isolated or so numerous as to fill the entire cyst. In one case of contiguous cysts, an epithelial cell was found to form thyloses in both cysts — in the one case giving rise to an isolated cell, in the other forming a tissue which nearly filled the entire cavity.

In radial section the reservoirs are round or oblong cysts of variable size, and they are either contiguous or distant. In the former case they rarely or never become confluent, but they maintain their separate identity as in Sequoia and Tsuga. In the latter case the intervening region is occupied by an aggregate of resin cells in all essential respects like those in the same regions of Sequoia and *Tsuga mertensiana*, or like the aggregates which are generally characteristic of *Tsuga caroliniana*. The inner epithelium usually consists of short, cylindrical and strongly pitted cells which, in the second and third rows, become successively longer and less strongly pitted, so that those in the outer row may be identical in form and markings with the isolated resin cells. In the two outer rows the cells not infrequently show bordered pits on their radial walls, thus presenting transitional forms which gradually pass over into tracheids, and the one then replaces the other. The parenchyma tracheids, which are always most characteristic of the spring wood, are always distinguished by the presence of large and prominent bordered pits, but in addition they are sometimes broad and thin-walled, and lie in radial series.

From these facts it is clear that the secretory reservoirs of the three genera in question always take the form of closed sacs, which DeBary has already pointed out as a feature of certain Coniferæ (9, p. 440), and in order to clearly differentiate them from those which occur in the higher Coniferæ, I shall reserve for all such cases the term *resin cyst*. That such sac-like reservoirs represent the primitive form of the resin passage scarcely admits of question when we observe the various transitional forms which they present and the relation they bear to the resin passages of the higher Coniferæ — a view which is strengthened by the observation of DeBary (9, p. 443) that primitive forms of the secretory reservoir occur in the pith of Ginkgo in the form of elongated sacs.

DeBary has shown (9, p. 440) that the secretory passages traverse the wood longitudinally, at first as prismatic tubes which usually acquire a round or elliptical, transverse section. This statement is applicable to Pseudotsuga, Larix, Picea and Pinus, but inasmuch as there are important differences of detail between

the first three genera and the last, in such a way that the former represent an intermediate, while the latter represents a completed type, it will be necessary to examine them separately. In all of these cases, however, the secretory reservoir is invariably characterized by the presence of a definite and continuous canal of indeterminate length, in consequence of which I reserve for them the appropriate and long used term, "resin passage," as distinguished from the resin cysts of the previously discussed genera.

In Pseudotsuga the resin passages are always scattering, though they frequently occur in tangentially extended groups of two or four contiguous or even coalescent reservoirs. The central canal, which is usually small and not infrequently very narrow, is rather more generally rounded than in previous types. The epithelium is very clearly defined and consists of one to three rows of thick-walled parenchyma cells, sometimes containing resin, the first row of which are rather small and radially flattened, but in *P. macrocarpa* they are rather thin-walled. In *P. douglasii* the epithelium is commonly extended on the two sides of the resin canal in such a way as to form a tangentially elongated tract which not infrequently extends beyond and involves neighboring medullary rays. In *P. macrocarpa*, on the other hand, the epithelium is concentric with the canal, thus forming a tract of about equal thickness all around. Such a deviation as is expressed in *P. douglasii* constitutes the first evidence of a tendency in development which is fully and frequently expressed in Pinus. Thyloses are of infrequent occurrence, and they appear to be confined to *P. macrocarpa*, where they are few in number and generally rather thin-walled. Parenchyma tracheids are usually not apparent in a transverse section. This results from the frequent location of the resin passages in the summer wood, which is not favorable to their development, and from the close resemblance which they bear to the tracheids of the spring wood; and while such elements form an integral part of the resin passage, their particular disposition cannot be exactly defined, though there is no good reason for supposing that they differ in this respect from what may be observed in other cases. In a longitudinal section the

canal is found to be more or less continuous, though it presents frequent constrictions, and it is thereby reduced to very narrow dimensions. It is this feature which causes the canal to exhibit such marked variations in size when seen in transverse section. The epithelium cells are narrowly cylindrical and rather long and thick-walled, as well as somewhat strongly pitted. Outwardly they become much longer and relatively narrower, and they eventually merge with the surrounding parenchyma tracheids by which they may also be replaced.

In Larix the same features of contiguity and coalescence may be observed, except that in *L. occidentalis* the resin passages sometimes form into continuous zones of imperfectly organized structures with the aspect presented in *Tsuga martensiana*. The epithelium is always well defined (Fig. 47) and it consists of one, sometimes two, rows of cells. The cells of the first row are small, very variable in form and size, thick-walled and more or less strongly flattened radially. They are also commonly resinous and more or less strongly pitted. When there is a second row of epithelium, the cells are essentially like the wood tracheids, and like the parenchyma tracheids from which they may be separated with difficulty. The latter, therefore, which are absent from the summer wood, can be distinguished from the elements of the spring wood only when the pits on the terminal walls (Fig. 47 *pr. t.*) are brought into view, or, more rarely, when the pits on the tangential walls are in evidence. Thyloses rarely occur, and so far they have been noted only in *L. occidentalis*, where they

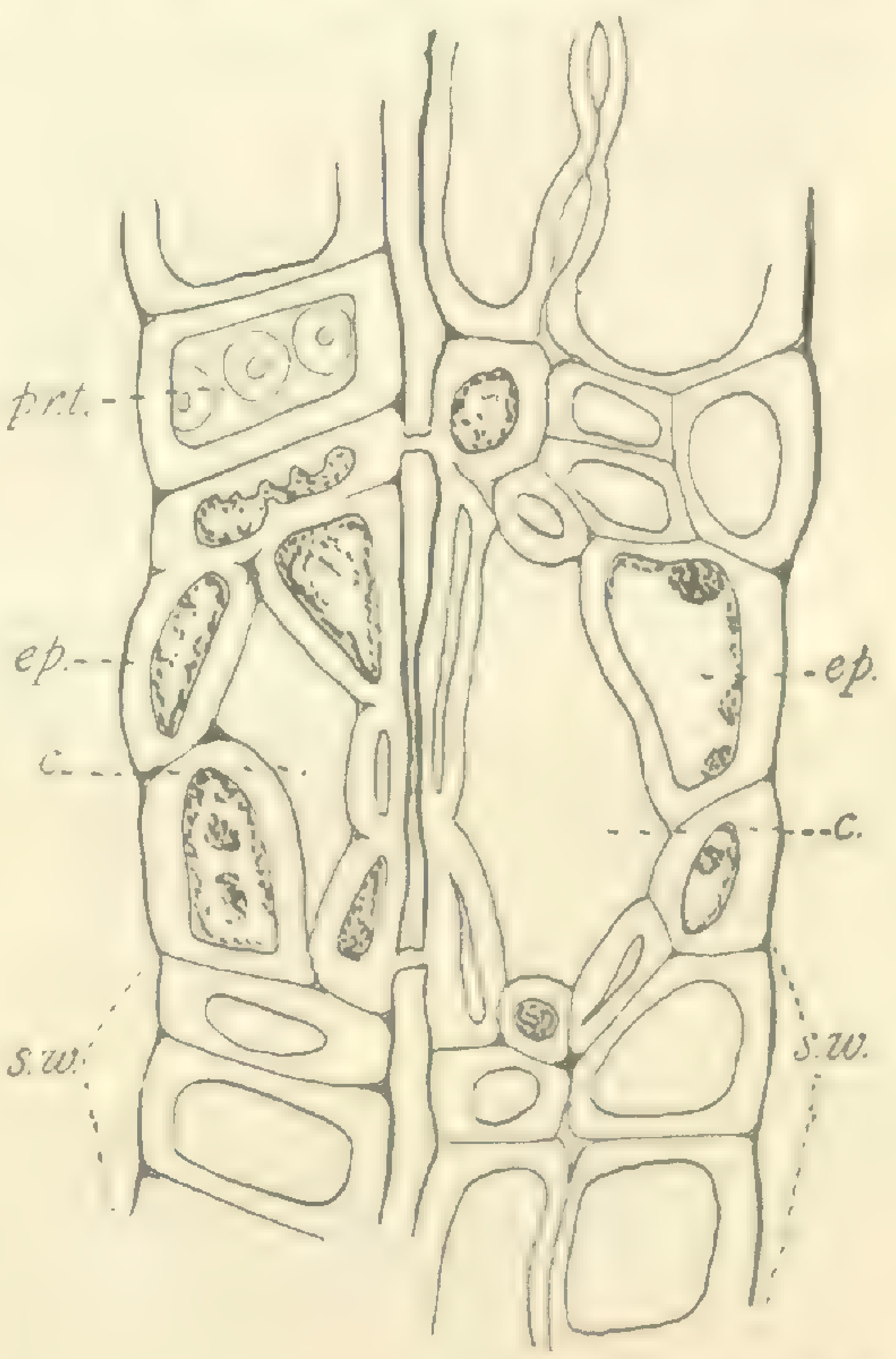

FIG. 47.—*Larix occidentalis.* Transverse section from the inner spring wood showing a pair of resin passages with the central canals (*c*); the thick-walled epithelium (*ep*); a parenchyma tracheid at (*pr. t.*) and the summer wood (*s. w.*). × 300.

are infrequent and thick-walled, and in *L. americana*, where they are of rare occurrence and thin-walled. In longitudinal section the central canal is always continuous, though constricted at intervals, a feature in all essential respects the same as in Pseudotsuga. Radially, the first row of epithelial cells are short cylindrical, or in *L. occidentalis* short fusiform, but there is a graduated increase in length outwardly, so that in the second, or in the third row if present, they become narrow and very long, and they eventually merge with the parenchyma tracheids through intermediate forms with bordered pits. All of the epithelial cells are thick-walled and strongly pitted, and they thus offer a somewhat strong contrast to the rather thin-walled parenchyma tracheids with bordered pits.

The resin passages of Picea differ from those of Pseudotsuga and Larix in being more strictly segregated, and in consequence there is a conspicuous absence of contiguous structures, which may nevertheless sometimes be seen in *P. nigra*, and especially of coalescent forms. They are usually narrow, but well rounded or oval, and there is far greater uniformity of structure and form than in any of the preceding types. The epithelium consists of one row, one to two rows, or even one to three rows of cells, differences which apparently belong to particular species, though no attempt has been made to define the precise limitations of such features. The cells are generally small, round or radially flattened and thick-walled, though occasionally a cell may be thin-walled as in *P. alba*. In cases of thick-walled epithelium, the outermost cells merge with similar tracheids from which they are not readily distinguishable, while the general epithelium becomes extended into a tangentially elongated tract as in *Pseudotsuga douglasii* and Pinus. Thyloses have been noted as of occasional occurrence in *P. nigra*, *P. pungens* and *P. sitchensis*, but they are always thin-walled. Parenchyma trachieds are not obvious in the summer wood, but they are recognizable in the spring wood where they appear to replace the resin cells, though they are apparently of much less frequent occurrence than in the genera previously discussed. In *P. alba*, however (Fig. 48, *pr. t.*), we sometimes find a radial series of tracheids which also extends laterally so as to form an enclosing

layer. Radially the canal is continuous, but with more or. less frequent constrictions as in Pseudotsuga and Larix. The epithelium consists of narrow, cylindrical and much pitted cells which increase in length in the outer layers where they become five to seven times longer than broad, and finally they merge with the parenchyma tracheids which replace them.

While the general composition of the resin passage in Pseudotsuga, Larix and Picea is the same as that of the resin cyst, it is obvious that the frequent constrictions in the canal indicate a partial survival of the cystic formation. We must therefore regard these structures and the three genera to which they belong as forming a transition group between the primitive resin cyst on the one hand and the perfectly organized resin passage of Pinus, with its canal of uniform width, on the other.

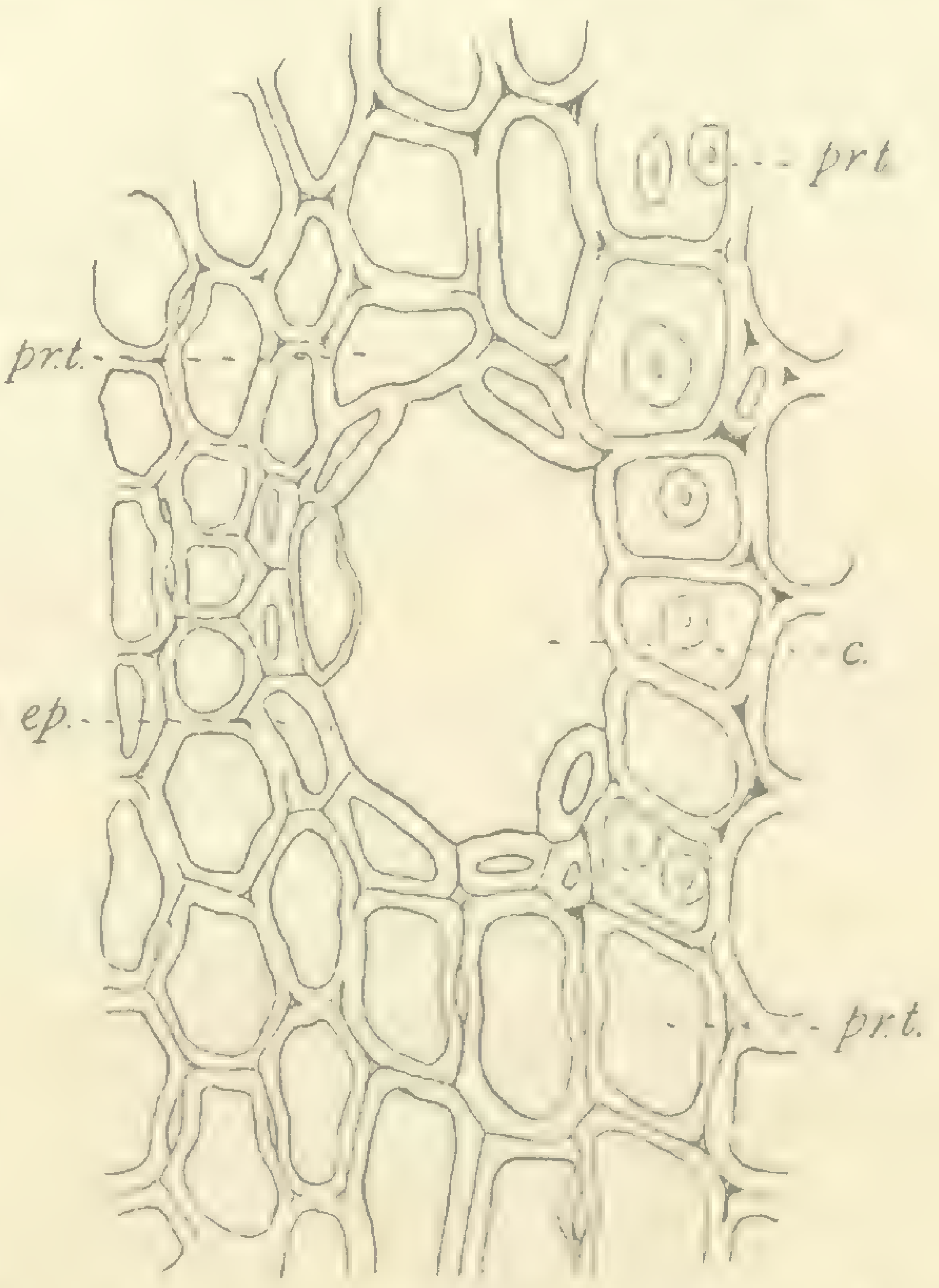

FIG. 48.—*Picea alba.* Transverse section of a resin passage from the spring wood, showing the central canal (*c*); the thick-walled epithelium (*ep.*) and the parenchyma tracheids (*pr. t.*). × 50.

In the genus Pinus, the resin passages show considerable variation in detail, but they all conform to the same structural type (Fig. 49). The central canal is broad and round, often very large, and in longitudinal section it is a perfectly continuous passage of uniform width. The epithelium consists of large, but very variable and thin-walled cells in one to several rows. In the soft pines it generally forms a concentric zone of uniform width, but in several of the hard pines there is a marked tendency to extension in a tangential direction and the formation of rather extensive eccentric tracts. In all of the pines there is a pronounced tendency for the epithelial elements to become so thin-walled that they are readily broken out in

making sections, while in the hard pines, as *P. cubensis*, *P. tæda*, *P. pungens*, etc., the cells are often strongly resinous. In the outer epithelium, the thin-walled elements may be associated with occasional thick-walled elements with which they are interchangeable, precisely as in the similar relations displayed by the medullary rays of *P. pungens* and *P. cubensis*. In the same region also there is a similar association with and transformation

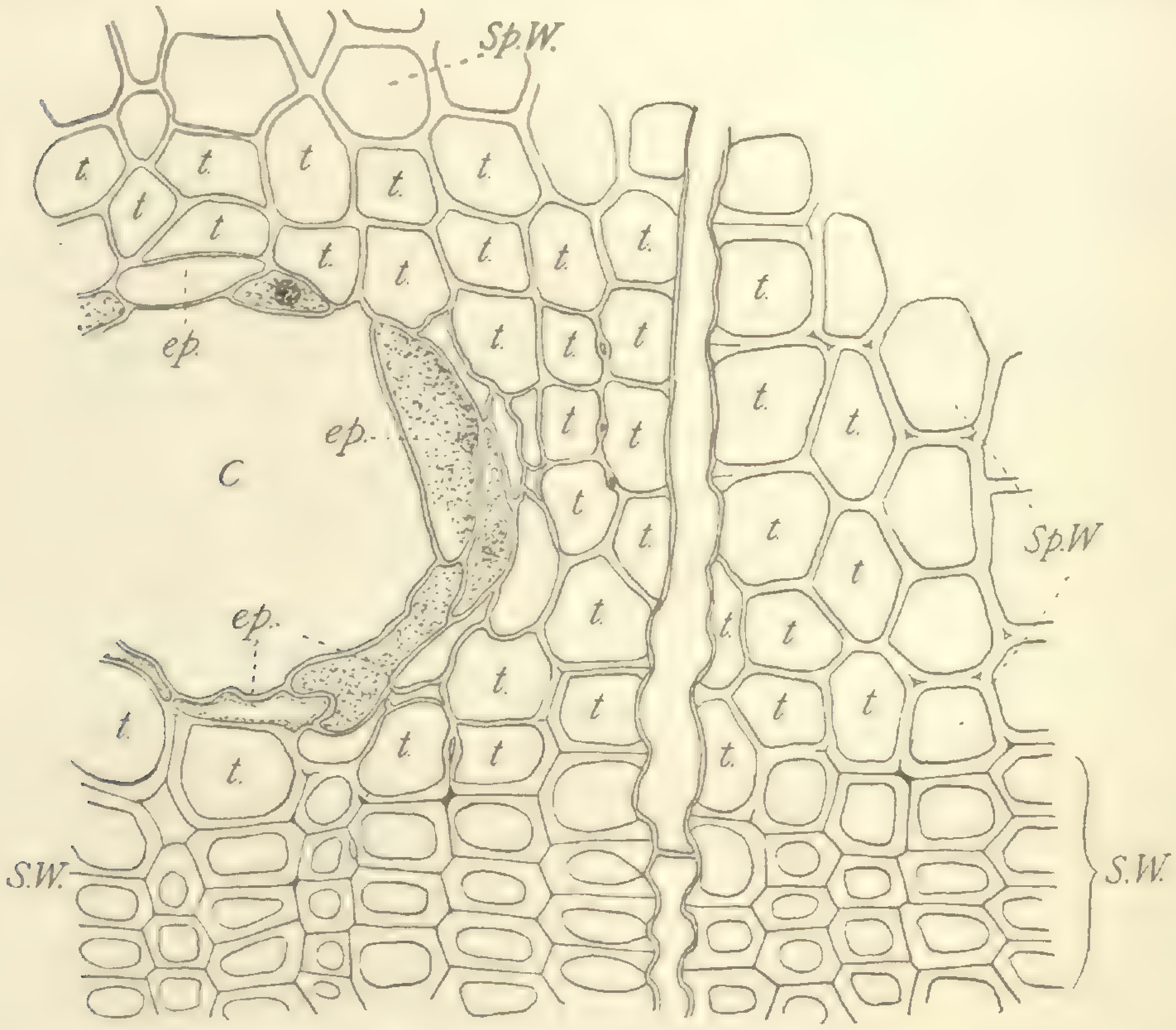

FIG. 49.—*Pinus reflexa.* Transverse section of a resin passage from the inner face of the sping wood showing the central canal (*C*); the thin-walled and resinous epithelium (*ep.*); the parenchyma tracheids (*t*); the spring wood (*Sp. W.*) and the summer wood (*S. W.*). × 225.

into parenchyma tracheids, which also has its parallel in the medullary ray. Somewhat more specifically, special reference to two examples may serve to illustrate the general nature of some of the more important variations. In longitudinal section the parenchyma tracheids are usually of much greater length than the associated parenchyma cells, with which they are parallel or coterminous, and they occur in large numbers in *P. lambertiana*. In *P. reflexa* they are coterminous with parenchyma cells which they finally succeed, to be replaced in turn by thin-walled wood tracheids. In *P. lambertiana* they are

always to be distinguished by the bordered pits on the radial, tangential and terminal walls, while in *P. reflexa* they are characterized by the large number of bordered pits on the radial walls, with very few on the tangential walls. In the former situation the pits are much smaller than in adjacent wood tracheids. Together with adjacent wood tracheids, the parenchyma tracheids may be more or less involved in bearing resin (*P. lambertiana*), while finally, as exhibited in transverse section, their numbers may be so large that they form extensive areas about the resin passage (Fig. 49). In such a case the sequence of elements in transverse section would be :—

1. Canal with thyloses.
2. Thin-walled epithelium.
3. Epithelium — cylindrical parenchyma tracheids.
4. Parenchyma tracheids.
5. Wood tracheids with thin walls.

Thyloses are a constant feature in the structure of the resin passages of Pinus (Fig. 30). They are always thin-walled and completely fill the canal. So constant are these features in association with those previously recounted that they serve to afford a ready means of accurately recognizing the genus under all circumstances.

The general course of development thus outlined shows that the parenchyma tracheid stands in such relation to the organization of the resin passage that its more frequent occurrence is directly correlated with a higher type of organization and development in the plants to which they belong.

We are now in a position to present a general summary of the relations which the resin cells bear to the organization of the secretory reservoirs — cysts and passages — and the position which the latter occupy in the economy of the plant, as follows:

1. Resin cells, which are of the nature of wood parenchyma, at first occur as isolated structures filled with resin, but they show a definite tendency to association, and later form definite aggregates.
2. Parenchyma tracheids become associated with such aggregates for the purpose of effecting a more complete nutrition of the secretory cells.

3. Resin cells, when aggregated beyond a certain point, develop schizogenous, intercellular spaces which form either central, closed cysts, or central canals of indeterminate length.
4. The structure of the cyst or passage always presents the same sequence of elements, and the work of the reservoir is then divided between
   (a) the tracheids which provide nutrition for the secretory cells;
   (b) the secretory cells or epithelium in which the formation of the resin takes place;
   (c) the cyst or canal which provides an outlet or storage reservoir for the surplus product;
   (d) the thyloses which may impede the proper storage of the resin, or which may individually serve the purpose of storage.

So long as the formation of resin is not excessive, it is stored in the cells where produced. This is true of all isolated resin cells, as well as of many which enter into the composition of complex cysts and passages. When the resin is excessive, however, the surplus is excreted into specialized reservoirs of the form of closed cysts, or of canals, and we are led to interpret the appearance of these structures in the higher Coniferæ as a response to such needs. The development of the resin passages will thus be seen to stand in direct relation to the capacity of the plant as a resin producer — a fact which is otherwise apparent from our knowledge of the general capacity of the different genera as resin producers, and a comparison of this feature with their known position in the line of descent.

(*To be concluded.*)

A LIST OF BERMUDIAN BIRDS SEEN DURING JULY AND AUGUST, 1903.[1]

HAROLD BOWDITCH.

The following list comprises those birds which fell under my personal observation on or near the Bermuda Islands between the sixth of July and the twenty-second of August, 1903, the time of my stay at the Bermuda Biological Station. The names of such birds as are included in the Check-list of the American Ornithologists' Union are preceded by their respective check-list numbers, and every effort has been made to bring the scientific names down to date. I wish here to express my thanks to Prof. Edward L. Mark, Director of the Biological Station; Mr. John T. Nichols; Mr. Owen Bryant; Mr. Goodwin Gosling, of Hamilton; and the Messrs. Louis L. Mowbray and R. S. McCallan, of St. George, for their valuable aid in furthering my observations.

70. *Sterna hirundo* (?) Linn. Common Tern. — Terns were seen three times off the north shore, in each case a single individual, but not once was I near enough to make a positive identification. They were in all probability *S. hirundo.*

89. *Puffinus gravis* (?) (O'Reilly). Greater Shearwater.—A Shearwater-like Petrel (family Procellariidæ) was seen in sight of Bermuda, July sixth; it was probably a Greater Shearwater, although certain identification of this bird and of the two others seen on the same day would not be possible without specimens.

109. *Oceanites oceanicus* (?) (Kuhl). Wilson's Petrel.— A "Mother Cary's Chicken" was seen from the S. S. "Gladisfen" on the "Challenger" bank, about twelve miles southwest of Gibbs' Hill, on the first of August. Identification was impossible, but the bird was probably a Wilson's Petrel. Merriam ('84, p. 284) reports finding a Leach's Petrel, dead, on the

[1]Contributions from the Bermuda Biological Station for Research. No. 3.

shore at "'Tuckerstown Beach,' May 1, 1881," and says: "The bird is common enough at sea a hundred or two miles from the Bermudas, but I never saw one near the islands."

112. *Phaëthon americanus* Grant. Yellow-billed Tropic Bird; "Long-tail."— The Yellow-billed Tropic Birds were perhaps the most conspicuous birds in Bermuda until the middle of August, when their numbers seemed to decrease. These birds lay one egg with brown markings, in holes in the cliffs, almost always with no attempt at a nest; as they are very close sitters, many opportunities are offered for study at short range. Mr. Owen Bryant found chicks in the "natal down" on Castle Island on June thirtieth. Eggs were found in Harrington Sound as late as July twenty-sixth, and a downy young bird was found on Brangman's Fort on August twelfth.

I was very much interested in observing the change in the plumage of the young "Long-tail," as seen in many specimens. The bird emerges from the egg covered with puffy white down, shaded with gray on the wings, and has a pale grayish bill, gray feet, and gray, unfeathered lores. This "natal down" is changed for a plumage of white, with black spots on the head, wings and back, and one black spot on the end of each tail-feather. The bill is yellowish flesh-color and grayish; the lores are feathered, and the tail-feathers are all of the same length. During the persistence of this plumage, which in being speckled resembles that of the Red-billed Tropic Bird, the bill becomes yellowish orange, the tint which persists throughout life. The fact that I never saw a speckled bird on the wing, but always on the "nest," leads me to suppose that the speckled plumage is exchanged for a plumage indistinguishable from that of the adult bird, before the bird-of-the-year takes flight; and it seems as if the change could not be due to wear, as the bars and spots of black are almost half an inch from the ends of the feathers.

194. *Ardea herodias* Linn. Great Blue Heron.— I saw one of these birds in Tucker's Town Bay, July fifteenth, and another was seen on an island near Hamilton Harbor on the eighth of August. Capt. Savile G. Reid ('84, p. 242), quoting Major Wedderburn, says: "In 1846 the nest of this bird, containing two eggs, was found amongst the mangrove trees at Hungry Bay." This is said to be the only known nest-record.

234. *Tringa canutus* (?) Linn. Knot; Robin Snipe.— A single bird, probably of this species, was seen on July twenty-seventh on Cooper's Island, in company with three other waders, a Turnstone, a Spotted Sandpiper, and a supposed Sanderling. All were rather shy and hard to approach.

248. *Calidris arenaria* (?) (Linn.). Sanderling.—One instance, not a positive identification; Cooper's Island, July twenty-seventh.

263. *Actitis macularia* (Linn.). Spotted Sandpiper.—I have only two days' positive records for the Spotted Sandpiper, namely July twenty-seventh, when I saw two or three on Cooper's Island; and July twenty-ninth, two at Hungry Bay. However, Sandpipers were seen on one or two other days, and were probably the Spotted.

274. *Ægialitis semipalmata* Bonap. Semipalmated Plover: Ringneck.— One instance, a single bird on Cooper's Island, August twelfth.

283. 1. *Arenaria morinella* (Linn.). Ruddy Turnstone.— One record, Cooper's Island, July twenty-seventh.

289. *Colinus virginianus* (Linn.). Bob-white; "Quail."— According to Capt. Savile G. Reid ('84, p. 227) these birds were imported from the United States in 1858 or 1859. My records for them extend from July seventh to August twentieth, seldom more than one in a day. I heard the spring call as late as August tenth, and was told that a brood of young was seen near the Hotel Frascati, where the Biological Station was located, shortly before my arrival in Bermuda.

320b. *Columbigallina passerina bermudiana* (Bangs and Bradlee). Bermuda Ground Dove.— This is one of the common Bermuda birds, being found especially in cultivated areas. It is very tame, allowing one to approach within two yards of it.

428. *Trochilus colubris* (?) (Linn.). Ruby-throated Hummingbird.— On July twentieth, as I was driving along the Middle Road, not far from the Whitney Institute, a Hummingbird flew over my head from among some oleanders. As the Ruby-throat is the only Hummingbird that has been taken in Bermuda (Reid, '84, p. 210), the bird that I saw was probably of this species. On July fifteenth another member of our party (Prof. Albert Mann) saw a Hummingbird in the same neighborhood.

488. *Corvus americanus* Aud. American Crow.— Messrs. Bangs and Bradlee (:01, p. 253) say: ". . . . It is, however, doubtful if the Bermuda Crow is *Corvus americanus*. Its notes are said to be different, more like those of the European Carrion Crow (*Corvus corone* Linn.), a hoarse, raven-like croak.

During the season of 1900–1901, crows were seen but seldom and never more than three together at any one time. They were shy and their notes were not heard distinctly."

I have several records, namely: July seventh, several heard calling on Paynter's Hill; July tenth, two heard calling in the direction of Harrington Sound, from the Flatts; August tenth, a flock of seven seen at close range (but not heard) on the South Shore, about opposite the Devil's Hole; August eleventh, three together, seen and heard on the southern shore of Harrington Sound, west of Patton's Point; and August twenty-first, one heard from the Biological Laboratory on the side of a neighboring hill. In neither flight, appearance, nor voice did any of these crows seem to me to differ from *Corvus americanus*, and I heard their cawing distinctly, especially on July seventh and August eleventh. I was told that there were three Crows' nests on Trunk Island, Harrington Sound, and was shown a nest on Cooper's Island on July twenty-seventh, said to have contained young birds earlier in the season.

593. *Cardinalis cardinalis* (Linn.). Cardinal Grosbeak; Redbird.—The "Red-bird" is one of the most abundant of the residents, and I have an almost uninterrupted series of daily records from July seventh to August twenty-second, my entire stay, the single exception being on August first, which was spent on the "Challenger Bank," twelve miles from shore. At Hungry Bay I saw a Cardinal's nest containing three or more young birds, on July twenty-ninth, a late date, for Reid says ('84, p. 201), "As a rule, the two clutches of eggs are deposited about April 10th, and May 30th, respectively." Moseley ('79, p. 25) alludes to the fact that it is an introduced species, and Ridgway says (:01, p. 674), "the species is said to have been *introduced* from the eastern United States"; the date I am unable to determine.

Passer domesticus (Linn.). House Sparrow; "English" Sparrow.— Reid wrote in 1877 ('84, p. 196)[1] of two importations

[1]Reprinted from 1877.

from New York, one "a few years ago," the second in 1874, and says, "I have no doubt they will increase and multiply after their manner, and in time become as much a nuisance as they are now a curiosity." This prophecy has been fulfilled, and I am told that the "English" Sparrows breed in Bermuda at all seasons. The Sparrows are interesting in one respect, namely, the fact that the adult birds, and especially the females, are noticeably lighter and more yellowish than the United States birds. That this is due to bleaching is proven by a specimen taken by my friend, Mr. Nichols. This bird is an adult female, in which the light colored, worn-out tail feathers are being replaced by a new set of typical dark ones.

Carduelis carduelis (Linn.). Goldfinch.—Reid ('84, pp. 196–197) says, "I observed a single specimen of the European Goldfinch, *Carduelis elegans*, near Harrington Sound, in April, 1875; it was very wild, and I could not get near it, but I imagine it must have been an escaped prisoner." This bird is now common in Bermuda, and I did not find it at all hard to approach, in spite of the fact that Bangs and Bradlee (:01, p. 256) state that it "is exceedingly shy and wary." By far the largest flock that I saw was at the Flatts, on August tenth, and contained about thirty birds. On June twenty-ninth Mr. Owen Bryant found a newly built nest of the Goldfinch on Trunk Island, Harrington Sound; it was in a cedar, some twenty-five feet from the ground and six or seven feet from the trunk of the tree. On July sixth it contained four eggs.

611. *Progne subis* (?) (Linn.). Purple Martin.—On August fourteenth, while between Coney Island and the Ferry Reach, I saw two Martins flying past the Martello Tower, southward. I was unable to determine the species, whether Purple or Cuban, but as the range of the Cuban Martin is, according to Chapman ('95, p. 320), "Southern Florida south to Cuba and probably Central America," the birds were in all likelihood Purple Martins. Reid ('84, p. 190) states that this bird "has only .... appeared on one occasion, during the 'entrada' of September, 1849, when it was numerous." I looked this matter up in the "Natural History of the Bermudas," a collection by Miss H. T. Hurdis of scattered notes by her father, John L. Hurdis. His

only records of specimens fall in September, 1849, but he records martins seen by other people three times, viz.: August, 1847 (p. 26); September 19th, 1850 (p. 193); and April 24th, 1851 (p. 212).

631b. *Vireo noveboracensis bermudianus* (Bangs and Bradlee). Bermuda White-eyed Vireo; "Chick-of-the-village."— This bird ranks with the Cardinal and the Catbird in point of numbers; everywhere that one goes, he hears its characteristic song, translated into "chick-of-the-village" by the negroes. Bangs and Bradlee (:01, p. 253) say, "The iris in *V. bermudianus* is *white* as in *V. noveboracensis*, and not "brownish, brownish gray, or gray," as stated by Capt. Reid. This seems to me to be a very hasty conclusion, as I have never seen a Bermuda Vireo with a pure white eye. The birds are very tame and familiar, and I made it something of a point to look at the iris whenever a good opportunity offered, with the result that I saw just two specimens with "dirty white" irides, and these had every appearance of being young birds. The irides of all the other birds of which I took note were dark.

Reid ('84, p. 192) says, "It is on record that the newly fledged young of this species have been found entangled in the meshes of the web of the 'silk' spider, *Epèira* [Epeira] *clavipes*. These webs are of great size and strength, extending for many feet between adjoining cedars, and the number of them among the woods in summer and autumn is almost incredible. In all my rambles, however, I never met with an instance of poor little Vireo having walked into Epëira's parlor."

On the twenty-ninth of July I saw, at the edge of the mangrove swamp at Hungry Bay, a Vireo with a large mass of cobweb on the side of its head, completely covering the right eye. The left eye only was used, which necessitated the bird's turning on its perch in order to watch us, instead of simply turning its head.

704. *Galeoscoptes carolinensis* (Linn.). Catbird; "Blackbird."— Extremely common throughout the islands. During my stay in Bermuda I did not once hear the "mew" which gives the Catbird its name, and the song and the other notes of the Bermuda Catbirds sounded to me not quite identical with those of United States birds.

766. *Sialia sialis* (Linn.). Eastern Bluebird.— A very common bird. Bangs and Bradlee (:01, p. 255) state that the Bluebird is migratory as well as resident, so that "possibly some of" the migrants "remain and breed and thus counteract any tendency to vary that the island birds might develop if wholly cut off from the main body of the species." Reid ('84, p. 175) says of the nests, "I have found them commonly in holes in old quarries or roadside cuttings; also in crevices of walls; in rocks, even when some little distance from the shore; in holes in trees; on the branches of trees; in stove and water pipes; in calabashes, boxes, etc., hung up for them in the verandas of houses, ... and in several other curious situations."

On July tenth Mr. Owen Bryant found a Bluebird's nest containing three young birds, built in the capstan of an old wreck near Coney Island. On the twenty-sixth of July Mr. John T. Nichols and I found some holes in a bank of sand, part of one of the cliffs nearly due north from the Devil's Hole, Harrington Sound; they were some four or more inches in diameter and a foot and a half to two feet deep, and two of them contained nests of soggy vegetable materials, one of which had in it a couple of bad eggs, probably Bluebirds'. This seemed to us a strange nesting site for the bird which we always associate with the hollow limb of an old apple tree.

Besides the twenty-one birds listed above, the following were reported to me:

On July twenty-third Mr. Leon J. Cole saw a Tattler (*Totanus*), probably *melanoleucus*, at St. David's.

During July a large Hawk was seen by various members of the Bermuda Biological Station. His identification as a *Buteo* was all but complete.

On August sixteenth Mr. Louis L. Mowbray told me of a Snowy Owl (*Nyctea nyctea*) which had been seen on the afternoon of the previous day, in the Devonshire marsh. Swallows (probably Barn Swallows, *Hirundo erythrogastra*) were reported common.

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[1] Note.— This paper by A. H. Verrill, seems to have been overlooked by the author.— E. L. Mark.

Neritina virginea. *variety* minor.

X 2 DIAMETERS.

NERITINA VIRGINEA VARIETY *MINOR*.[1]

MAYNARD M. METCALF.

WHILE collecting one summer in Jamaica, W. I., the author visited the "Salt Pond" near Port Henderson. This shallow pond is separated from the ocean by a narrow strip of sand over which the waves break during heavy storms. It has no outlet to the ocean and no fresh water streams flow into it. The water thus comes to be considerably more salt than that of the open ocean. The sample of water from these ponds which the author examined had a specific gravity of 1.038.

The fauna of this pond is quite rich and includes some very interesting forms. One is especially attracted to the beautiful little Neritina which literally covers the beach for rods near the water's edge. From a double handful of these animals scooped up in one spot on a little sand bar near the shore, the author has selected the shells in the accompanying plate. They are arranged for use in another publication and are designed to show a remarkable example of diversity. I would like here to call attention not only to the diversity but also to the dwarfing of these shells and its apparent cause.

Neritina virginea is a widely distributed littoral marine species. Full grown adults from the ocean are of the size of the figures on the accompanying plate. They show the same types of color and color pattern. Other types also are found among both the open ocean shells and those from the Salt Pond, but I have not attempted to figure them.

It is interesting to find that the Neritina of the "Salt Pond" is a dwarf variety. In almost every regard except size the animals resemble their ocean relatives, but their size is much less. The diameter of an average sized shell from the Salt Pond

[1] By the courtesy of The Macmillan Company the author is permitted to use for this article the accompanying plate which he has prepared for use in *An Outline of the Theory of Organic Evolution*, now in press.

would be about half that of an average shell from the open ocean. The figures on the plate are enlarged two diameters.

Apparently the extra salinity of the water in the Salt Pond has dwarfed the animals. That they are not young individuals is indicated by the facts (1) that no individuals of larger size were found, (2) that no smaller ones were found, indicating that they were not breeding at the time these shells were gathered. It can hardly be supposed that both the very young and the adults hide themselves from view, while the half-grown individuals crowd upon the shore in numbers that literally cover the sand at the water's edge. Yet the author should mention that he has seen a letter to Professor E. A. Andrews in which reference was made to these shells, called by the natives *Bossu*, saying that they are used for food and are gathered in fresh water streams at night with lanterns, but that during the day they hide under stones and can be found only with difficulty. There seems little doubt that the form from Salt Pond Neritina is a dwarf variety, and if so, the most probable cause of the dwarfing seems to be the density of the water in which they live.

It is still more interesting to find that a similar dwarfed Neritina occurs in fresh water streams in Jamaica. Professor Andrews has collected them in a small stream at Port Antonio, and the same letter referred to above mentions their occurrence in Mabess River, a branch of Spanish River near Buff Bay. Doubtless they occur in other Jamaica streams.

The author has about five hundred shells collected for him by Dr. F. S. Conant in "a small stream at Port Antonio," probably the same stream in which Professor Andrews saw them. These shells are all small, — no larger than those from the Salt Pond. Among them are some that are very small and apparently immature. Careful search should be made for full sized individuals in these streams before we can be positive that none are present. This the author has been unable to secure. Such data as we have, however, especially in comparison with the Salt Pond conditions, seems to indicate the probability of these fresh water Neritina shells being a dwarf variety.

If this conclusion is correct we have the very interesting phenomenon of an animal normally living in the ocean able to adapt

itself to life in fresh water or to water of greater salinity than that of the ocean, but unable to attain its full size except in the ocean.

The dwarfed forms may fairly be called a variety, though their difference from the ocean forms be only one of size probably directly due to increased or decreased salinity of the water in which they live.

The great diversity in color and in color pattern found in *Neritina virginea* is well known, yet it may be worth while to call attention to the completeness of the intergrading between any two types, however divergent.

Color shade. — Note first the differences in the ground color of the shells: yellow in 5*b*, 19, and 22; white in all the rest. Observe that the colored lines are black in 1, 3, 5, 5*b*, 6, 6*a*, 19, 20, 22; purplish in 6*b* and 11; red in 7*a*; gray in 23; black and red in 2; that the major lines are black and the minor lines red in 1*a*, 3, 3*a*, 4, 4*a*, and 5*a*; that the major lines are black and the minor lines purple in 4*b*, 17 and 16.

Color pattern. — 1 is marked with a few heavy lines. From 1 to 6 these major lines become broken up into small V-shaped loops. In the shells *a* accessory minor lines are added. In the shells *b* these are more numerous.

Series 9 to 14 shows diversity in the pattern near the apex of the coil: 9 has a few slightly larger white dots near the coil, 10 has larger dots here, 11 has them very large; in 12 they have united to form a continuous white band; in 13 and 14 this band is wider.

Series 15 to 24 shows diversity in the character of the equatorial light band. In 15 and 16 only the minor lines are interrupted or faint along the equator of the shell; in 17 the major lines also are interrupted; in 18 the band is almost clear white; 19 and 20 show narrower bands; in 21, 23 and 24 the equatorial band is shown by a difference of color in and under the pattern; in 22 the equatorial line is faintly indicated in the pattern itself, being bordered above and below by large, heavy, black loops.

The shells figured are but a few selected from the large number collected. Other types of color and of color pattern were

found. Between any two of the shells collected, no matter how divergent in type, a completely intergrading series could be found.

It is doubtful if these colors and color patterns are of protective value. The shell is enclosed by flaps of the mantle most of the time rendering the coloration invisible. Also all types of color pattern are seen in one locality. Then, too, the animals are in such great numbers that they could hardly escape the observation of their predatory enemies, if such they have, by means of their coloration.

The shells shown as numbers 5*b*, 8*b*, 19 and 22 are from Port Antonio, probably from the stream in which Professor Andrews found Neritina, a small shaded stream with a dark bottom of vegetable mould. One can readily observe that the shells from the Port Antonio stream are darker than those on the unshaded, light-colored sand beach of the Salt Pond. Few of them resemble numbers 1 to 5 or the *a* shells of the accompanying plate. Most are heavily marked with dark lines, many of the type shown in 8*b* being found. As a whole, the shells from the stream average much darker than those from the Salt Pond. Also it is noticeable that the ground color of almost all of these fresh-water shells is yellow, while that of the Salt Pond shells is white.

Remembering that it is doubtful if the coloration of these shells is to any considerable extent protective, it is interesting to find that the darker-colored shells are found in the midst of dark-colored surroundings, in a shaded stream, while the lighter-colored shells are from an unshaded beach of light-colored sand.

Comparison with the collections of *Neritina virginea* in the United States National Museum and in the Museum of the Philadelphia Academy of Sciences shows that the color of the Jamaica Salt Pond shells averages considerably lighter than that of shells from the ocean, the ground color being a clearer white, and shells of the patterns represented in figures 1 to 6 and 1*a* to 6*a* being present in larger proportion.

Few, if any, finer examples of diversity in color and in color pattern are known. The same types of coloration are found in the full grown shells from the ocean. In the absence of breed-

ing experiments, if it were not for the completely intergrading forms, systematists would probably have no hesitation in recognizing several species. As it is, all must without doubt be included in one species, and it seems hardly worth while to name as varieties (*punctata*, *lineata*, *bilineata*, *trilineata*, etc.) even the most divergent types. The dwarf forms, however, might fairly be called variety *minor*.

The writer would suggest that, if the difficulty of rearing these animals be not too great, it is probable that they would be favorable subjects for breeding experiments.

The Woman's College of Baltimore,
April 25th, 1904.

STUDIES ON THE PLANT CELL.—III.

BRADLEY MOORE DAVIS.

Section III. Highly Specialized Plant Cells and Their Peculiarities.

Very much of our knowledge of the structure and behavior of protoplasm in plants has been derived from the study of certain cells whose organization has reached an exceptionally advanced degree of differentiation. The peculiarities of these cells are obvious and have proved of great interest but we have as yet scarcely made a beginning in the study which must trace and relate these characteristics of the most complex products of cellular evolution in plants to their more simple progenitors.

This section will describe in some detail the structure and protoplasmic activities of the following six highly specialized cells: 1, The Zoöspore; 2, The Sperm; 3, The Egg; 4, The Spore Mother-Cell; 5, The Cœnocyte; 6, The Cœnogamete.

1. The Zoöspore.

Zoöspores are interesting not only for their own peculiarities but also because they are well known to be the progenitors of the sexual cells or gametes which become later differentiated into the egg and sperm. Comparative studies upon three cells so closely related and yet so diverse in their extremes of structure are sure to yield important results.

The zoöspore is generally an uninucleate cell, colorless in the Fungi, but containing a chromatophore or plastids in all other groups of thallophytes. There are usually two or four cilia attached to the anterior pointed end which is free from coloring matter and at this region one may expect to find a red pigment spot. Some zoöspores are exceptional for special peculiarities, as those of Vaucheria which are multinucleate, each nucleus

being accompanied by a pair of cilia, or those of Œdogonium whose colorless forward end bears a crown of numerous cilia. The zoöspore stands among the higher forms for a type of motile organism that is very close to the bottom of the assemblage of groups and developmental lines which make up the Algæ. The forms most closely related to the zoöspore are in the family Chlamydomonadeæ of the Volvocales. But at this general low level of the plant kingdom there are several groups whose members pass most of their lives in motile conditions (Volvocales, Flagellates and Peridinales) and the cells of all of these types resemble zoöspores to a greater or less degree in their structure and habits, so that this condition represents a widespread and well defined stage of evolutionary development. Therefore when zoöspores are formed in the life history of some higher plant they represent a return on the part of the organism for a short time to the structure and mode of life of an ancestry perhaps related in some way to the groups that still have the motile habits throughout most of their existence.

For these reasons close comparisons in structure between the zoöspore and motile Algæ will be interesting and should help to explain the peculiarities of these cells. These peculiarities chiefly concern the organ that forms the cilia (blepharoplast), which becomes very complex in the sperm, and the pigment spot.

Unfortunately studies upon these problems have been few and we are not prepared to make a general statement of the conditions. The most recent investigation on the structure of the zoöspore is that of Timberlake (:02), but Strasburger has written extensively on the subject, especially in the *Histologische Beitrage* ('92 and :00). The later paper (:00, p. 177–215) reviews the entire subject of cilia formation. Dangeard has presented an account of the Chlamydomonadeæ, '99, and in :01 described especially Polytoma, comparing its structure with that of the animal spermatozoan.

Polytoma (see Fig. 9 *a*) is a colorless organism but its cell structure and life history place it unquestionably among the Chlamydomonadeæ. The two cilia arise from a small body (blepharoplast) situated at the extremity of the cell. A delicate

thread-like structure, which Dangeard calls the rhizoplast, extends from the blepharoplast into the cytoplasm and sometimes ends at the side of the nucleus in a granule (condyle). The cilia grow out from the blepharoplast. This apparatus is not known to bear any relation to centrosomes or to the kinoplasm of nuclear figures present at the time of spore formation. But it should be noted that the blepharoplast is situated directly under if not actually in the outer plasma membrane, which is kinoplasmic. The filamentous connection between blepharoplast and nucleus is probably important, especially since it has also been found in zoöspores (Timberlake, :02, for Hydrodictyon) but we do not even know its developmental history much less its function. Further study will be necessary to make clear possible relations to kinoplasm around the nucleus or to centrosomes. Consequently Dangeard's comparison of Polytoma to the animal spermatozoön is not convincing for it seems to be established for the spermatozoön that portions of the middle piece at least and the flagellum are derived from a true centrosome. Indeed from the meager evidence now at hand the blepharoplast of Polytoma is as likely to be a structure differentiated from the plasma membrane as to have any relation to the nucleus. But detailed studies on sporogenesis may discover a history more in harmony with that of Hydrodictyon.

We have summarized a portion of Timberlake's (:02) account of sporogenesis for Hydrodictyon in the previous section under the head of "Cleavage by constriction." We shall consider now certain details. Small spherical bodies are found at the poles of the spindles during nuclear division in the mother-cell. They are undoubtedly accumulations of kinoplasm and perhaps stand for centrosomes. However they have no polar radiations nor could they be followed between mitoses when the nuclei were in resting conditions. It is not probable therefore

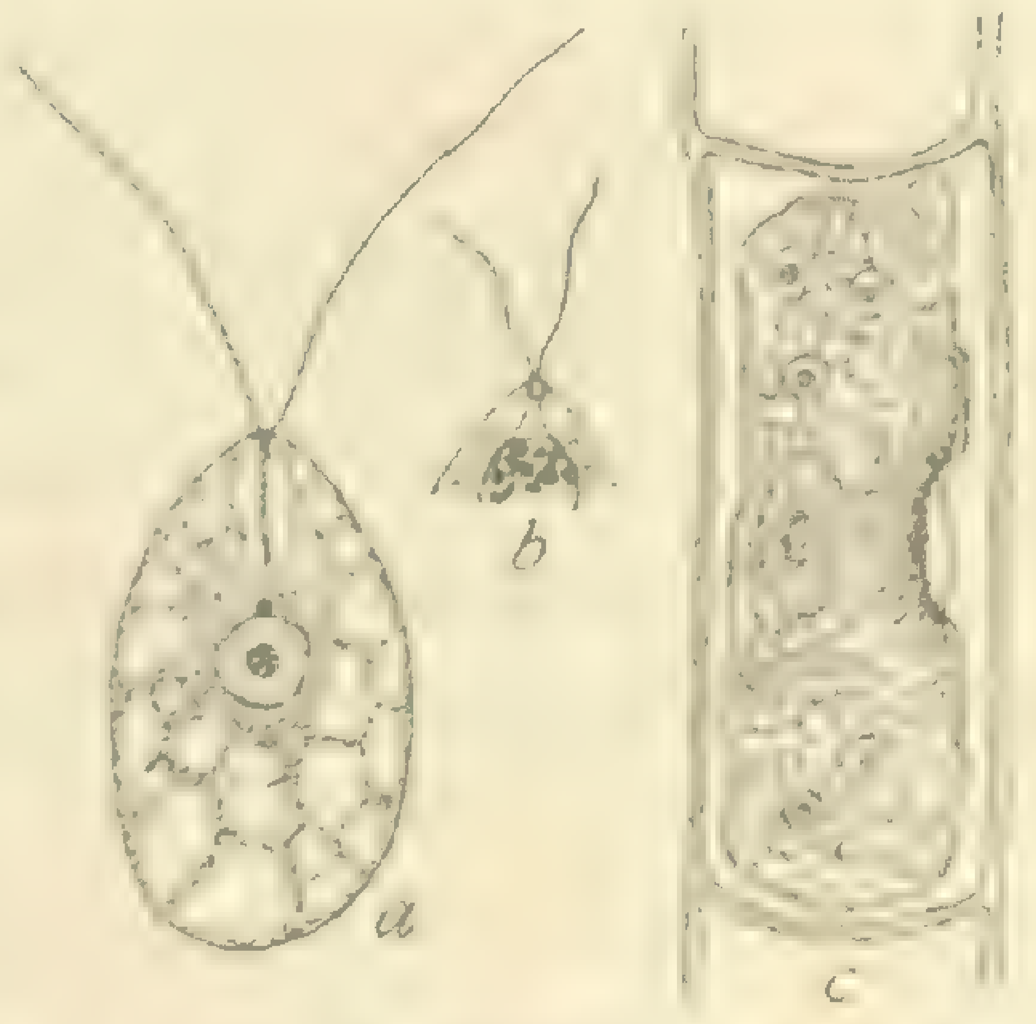

FIG. 9.—The Zoöspore. *a*, Polytoma; *b*, Hydrodictyon; *c*, Development in Oedogonium. (*a*, after Dangeard: 01; *b*, Timberlake: 02; *c*, Strasburger '92.)

that these structures are permanent in the cell. After nuclear multiplication is ended segmentation proceeds until the nucleate masses of protoplasm separate from one another as zoöspores. Then a body may be found lying in contact with the plasma membrane and bearing a pair of cilia (Fig. 9*b*). This basal body (blepharoplast) by its reaction to stains seems to be entirely distinct from the plasma membrane and is connected with the nucleus by very delicate threads. There is a time just previous to the differentiation of the zoöspores when the nuclei lie very close to the cleavage furrow that finally separates the adjacent zoöspore origins. A granule may sometimes be observed close to these nuclei and it is possible that this is the first appearance of the basal body (blepharoplast). If this should prove correct the structure may have a direct relation to the kinoplasm around the nucleus, a relation that is afterwards maintained through the two or three delicate fibers that connect these structures. Thus the blepharoplast if not directly derived from a centrosome may at least have its origin from the same region of kinoplasm. However these possibilities are mere speculations and the investigation of these points is very much to be desired in a number of algal and fungal types.

We are now brought to the views of Strasburger as expressed in his writings of '92 and :00. His investigations have been chiefly on Vaucheria, Cladophora and Œdogonium. In all of these forms the cilia come from a body (blepharoplast) which he believes to arise from the outer plasma membrane (Hautschicht). The nucleus lies close to the plasma membrane at the time when the blepharoplast is formed and may determine its development there as a dynamic center, but the blepharoplast is not a centrosome according to Strasburger. It is of course kinoplasmic since it develops from the plasma membrane and this would accord with its activities as a cilia forming organ. The blepharoplast is extraordinarily large in Œdogonium (see Fig. 9 *c*) and develops a ring of numerous cilia on the exterior while at the same time fibrillar rays grow back into the cytoplasm and probably help to give a compact organization to the zoöspore. This structure is very suggestive of the centrosphere and aster that cuts out the ascospore (see Section II, Free Cell

Formation) and in spite of Strasburger's conclusions that it is derived entirely from the plasma membrane we are justified in asking for a fuller description of its development. There is the possibility of a different origin wherein the nucleus may play an important part which, in the light of Timberlake's studies on Hydrodictyon, suggests that Strasburger may not have discovered the earliest beginning of the blepharoplast in Œdogonium. And the same doubts apply to Cladophora and Vaucheria.

There is thus considerable divergence in the views of the origin and nature of the blepharoplast in zoöspores, Strasburger believing that they are developed as a specialized region of the plasma membrane with no relation to centrosomes, and Timberlake holding that the structure in Hydrodictyon is not a part of the plasma membrane but comes from the interior of the protoplasm. The problem is also involved with conditions in the sperm, where there is likewise a difference of opinion as to the homologies of the blepharoplast but an undoubted origin at least in the pteridophytes and gymnosperms from the interior of the cell. We should naturally expect the blepharoplasts of zoöspores and sperms to be homologous and consequently the problem is of great theoretical interest and will be taken up again in our discussion of the sperm. Its solution demands a most thorough study of the development of some of the larger zoöspores as in Œdogonium and certain species of the Confervales and Volvocales.

The pigment spot is almost universally present in zoöspores and is also characteristic of the cells of many motile organisms as in the Volvocales and Flagellates while occasionally found in other groups. The structure has been called an eye spot from its fancied resemblance to the simple eyes of certain Crustacea (Cyclops, etc.) but this term is unsatisfactory since it is not established that the pigment spot is primarily a receptive organ for light or warmth; but even should it prove to be thus sensitive (which is very probable) thereby orienting the cell with respect to the direction of incoming rays, that is not a function comparable to sight.

The coloring matter of the pigment spot is held as a single globule or as a collection of numerous small granules in meshes

of the protoplasm. It is frequently associated with a plastid. The pigment may be readily broken down and dissolved out by such reagents as alcohol and ether. In chemical composition it is very close to hæmatochrome and thus may be related to chlorophyll or a derivative of that substance. The cytoplasm around the pigment spot is undifferentiated and when the coloring matter is removed it is very difficult and sometimes impossible to find the situation of the structure. Consequently the pigment spot can hardly be considered a protoplasmic organ since it is merely an accumulation of coloring matter at some point in the cell. Strasburger (:00, p. 193) states that the pigment spot of certain zoöspores (Cladophora, etc.) is formed in the plasma membrane but this is not true of many other motile cells (Flagellata) and there is no doubt that in some cells (*e. g.* the gametes of Cutleria) the pigment spot is a portion of a plastid. The literature upon the structure and function of pigment spots is reviewed by Zimmermann (*Beiträge z. bot. Centralb.* Bd. 4, p. 159, 1894) and since then Wager ('99) has presented a detailed study of Euglena.

2. The Sperm.

The sperm is unquestionably derived from the zoöspore through primitive types of gametes which were identical with zoöspores in all essentials of morphology. I have described the origin and evolution of sexual cells of plants in two recent papers (*Popular Science Monthly*, Nov. 1901, p. 66 and Feb. 1902, p. 300). We should expect the simplest forms of sperms to have the characters of zoöspores and this is the fact. The sperms of the Algæ, as a rule, have the same number of cilia (usually two) as their ancestral asexual zoöspores. They generally contain a chromatophore, although sometimes much reduced, and there is present the pigment spot. The cilia are attached at the pointed end or at the side, arising from colorless protoplasm that sometimes contains the pigment spot while the chromatophore, when present, and the nucleus lie at some distance from this region of the cell. The sperms of bryophytes and pteridophytes are much attenuated in form and lack the

pigment spot and chromatophore. Those of the bryophytes and the Lycopodineæ are biciliate while other pteridophytes have multiciliate sperms the cilia being distributed on a band (blepharoplast) which lies along one side of the spiral structure. A large portion of the spiral in these sperms is composed of nuclear substance and much of the remaining cytoplasm with granules and vacuolar inclusions may frequently be found in a vesicle attached to the larger end of the spiral.

The only motile sperm among the Fungi is that of Monoblepharis. The male cells of other Fungi are non-motile bodies (spermatia) generally formed from the ends of delicate filaments which are found in special organs called spermagonia. Spermagonia have been described in the Uredinales, the lichens and in the Laboulbeniaceæ but their function is only clearly established for the last two groups. They are very highly differentiated in the Laboulbeniaceæ and comprise several types of structure. Another type of male cell, found in certain groups of the Phycomycetes and Ascomycetes, is the cœnogamete (to be described presently) which is however not the homologue of the sperm but of the mother-cell or antheridium that develops such structures. Sperms of the red Algæ (Rhodophyceæ) are likewise non-motile and they are invariably formed singly in small cells at the ends of filaments. These non motile sperms of Fungi and red Algæ are exceedingly small uninucleate bodies without further complexity of structure as far as is known.

We shall not attempt to discuss the earlier literature that treats of the structure and development of the plant sperm. In 1894 Belajeff published a German translation of a paper written two years before in Russian which presents the views of previous investigators and to this the reader is referred for such historical references. At that time various opinions were held respecting the organization of the sperm, some writers (Campbell, Guignard and others) believing that it was chiefly or wholly nuclear in origin, while another group (Zacharias, '87, Belajeff, Strasburger, '92, etc.) thought that the cytoplasm shared very largely in its structure. Belajeff ('94a) from studies among the Characeæ showed with especial clearness that the cytoplasm was an important constituent of this sperm since the nuclear

material occupied a restricted region in the middle of the spiral structure. This was the first of a series of investigations which have given especial attention to cytoplasmic activities during spermatogenesis and placed the entire subject in a new light.

The year 1897 brought forth almost simultaneously three short papers by Webber ('97a, '97b, '97c) and Belajeff ('97a, '97b, '97c) respectively. Webber had studied the development of the motile sperms of Zamia and Ginko, Belajeff certain forms of the Filicineæ and Equisetineæ. These were of the nature of preliminary announcements and both authors published later more detailed descriptions and discussions. The discoveries of motile sperms in Ginko by Hirase and of Cycas by Ikeno were announced in several short papers during the years 1896 and '97 but without descriptions of their development. This literature together with later papers of Ikeno, Shaw, Belajeff, Hirase, and Fujii is reviewed in Webber's last contribution (:01) and also in Strasburger's discussion of "Cilienbildner" (:00, p. 177) to which the reader is referred for the most complete treatments of spermatogenesis in plants yet published.

The cycads and Ginko are the most favorable subjects known for studies in spermatogenesis. Detailed accounts of the cycads are given by Ikeno ('98b) for Cycas and by Webber (:01) for Zamia, these forms agreeing with one another in all essentials. Two sperms are developed from the daughter cells (spermatids) following the division of the so-called body cell in the pollen tube. The process really begins in the body cell with the appearance of the blepharoplasts. Their development has been followed with especial attention in Zamia. They are formed *de novo* in the cytoplasm at some distance from the nucleus and while the latter is in the resting condition. They appear independently of one another, generally on opposite sides of the nucleus but sometimes much nearer together (Fig. 10 *a*). Each is a large deeply staining body with numerous radiations extending into the cytoplasm. The blepharoplasts then increase in size and, moving farther away from the nucleus, take positions exactly opposite to one another. The nucleus of the body cell now divides, its spindle being clearly intranuclear (Fig. 5 *d*) and consequently holding no visible relation to the blepharoplasts

which lie at a considerable distance from the structure (Fig. 10 *b*). The latter cannot then be said to occupy the position of centrosomes in relation to this spindle. Meanwhile important changes, which are best known for Zamia, take place in the blepharoplast. In this type the structure forms a hollow sphere which breaks up into segments and finally into granules as mitosis proceeds. The radiations disappear without holding any apparent relation to the spindle. During telophase each of the two blepharoplasts

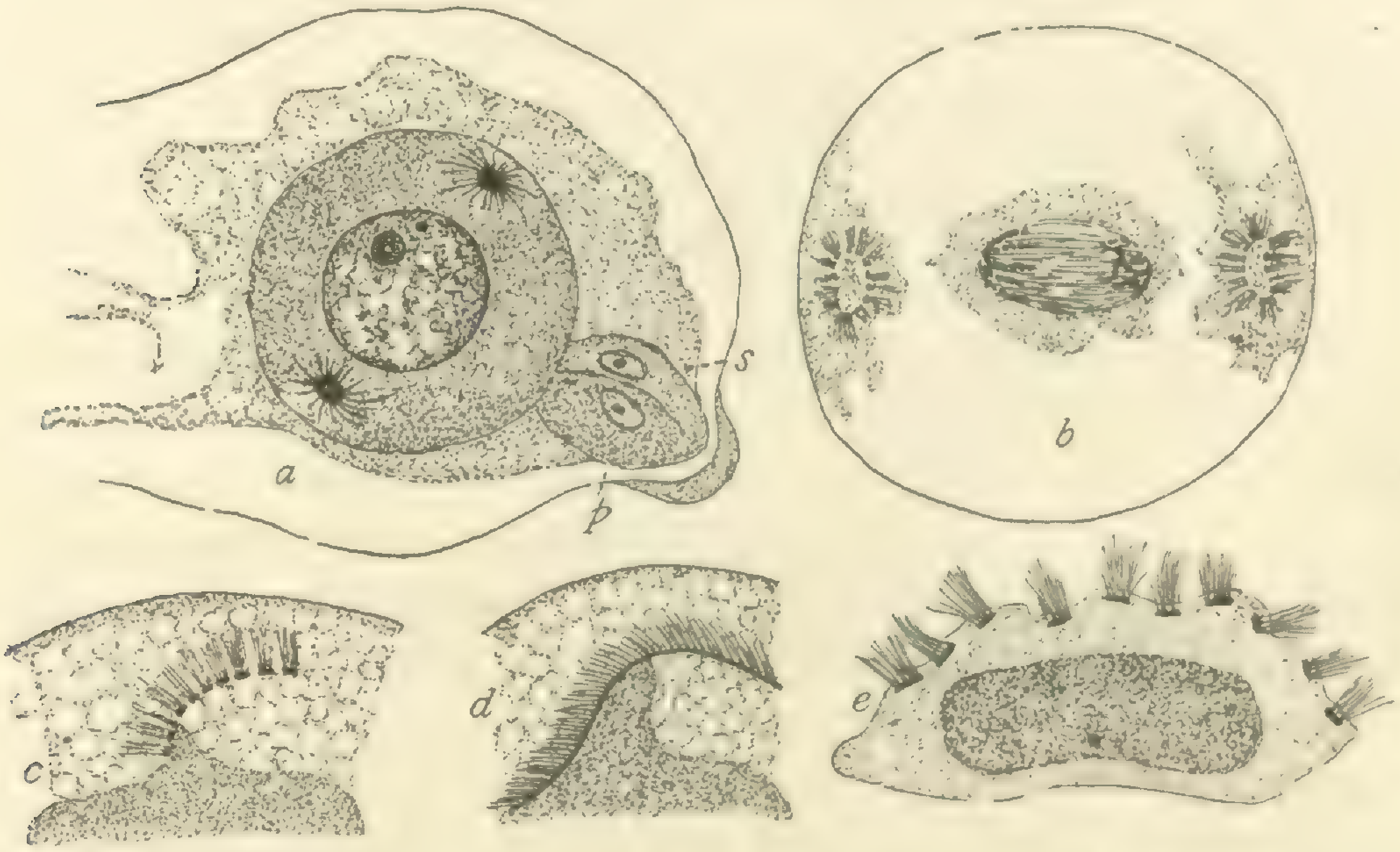

FIG. 10.— **Spermatogenesis in Cycas.** *a*, Body cell in pollen tube with two blepharoplasts; *s*, stalk cell; *p*, prothallial cell; *b*, anaphase of mitosis in the body cell the spindle lying between the two blepharoplasts which have begun to form cilia; *c*, Blepharoplast elongating, in contact with a process from the nucleus; *d*, end of blepharoplast attached to the nucleus at a later stage of development; *e*, sperm showing section of the flattened spiral blepharoplast with cilia projecting beyond the cell. (After Ikeno, '98.)

appears as a mass of granules at some distance from the daughter nuclei which are to become the sperm nuclei. As a result of this division the spermatids (sperm mother-cells) are differentiated. At the close of the mitosis the blepharoplast enters upon its functions of forming in the spermatid a cilia bearing band which is to lie as a spiral around the sperm. The granules first extend as a delicate deeply stained line towards the nucleus and then in the opposite direction. The nucleus in Cycas puts forth a papilla (Fig. 10 *c*) which meets this line of granules and remains attached to it for some time. The line thickens into a

band which lengthens and finally takes the form of a spiral of five or six turns which becomes more or less closely applied to the plasma membrane (Fig. 10 *c*, blepharoplast in section). The cilia develop as protuberances from the outer surface of the band (Fig. 10 *c* and *d*) and grow through the plasma membrane to the exterior of the cell. The nucleus in the meantime has increased in size until it occupies the greater part of the top shaped sperm (Fig. 10 *e*).

The history of spermatogenesis in Ginko is strikingly parallel to that of the cycads. The chief features were first described by Webber ('97c) and in greater detail by Hirase ('98). The two blepharoplasts appear *de novo* on opposite sides of the nucleus in the body cell. They show the same high state of differentiation as those of the cycads, being large and the center of a number of prominent radiations. Ginko however presents a peculiarity not reported in the previous group. A large spherical body lies between each blepharoplast and the nucleus in an area of granular cytoplasm. This structure stains deeply like the globules of nucleolar substance which are frequently found in the cytoplasm after nuclear division. They are probably accumulations of a somewhat similar material at these points in the cell to be utilized at later periods of spermatogenesis, since they decrease in size as the sperms mature. The spindle in the body cell is formed between the blepharoplasts but its poles lie at some distance from and are entirely independent of these structures. During this mitosis the spherical bodies pass to one side of the spindle so that the daughter nuclei (sperm nuclei) finally take the position formerly occupied by them. The blepharoplast becomes granular and begins to lengthen into a band, one end of which becomes attached to the nucleus that puts forth a small papilla towards the blepharoplast. The band elongates and takes the form of a spiral which makes several turns around one end of the cell just under the plasma membrane. Cilia then develop along this band as in the cycads. The earlier accounts, describing a short tail on the sperm were founded upon material that was not altogether normal and have been corrected by Webber and Fujii. The mature sperms have essentially the same form as those of Zamia and Cycas.

There has been some discussion on the morphology of these motile sperms of the gymnosperms. The claim has been made that they are ciliated spermatids (sperm mother-cells) and therefore different from the sperms of pteridophytes which are formed inside of mother-cells that upon their escape are left behind as empty cysts. However a close analysis of their structure will show that the sperms in both groups have an identical protoplasmic organization. There is a nucleus and a greater or less amount of cytoplasm in which the blepharoplast lies and the entire structure is surrounded by a plasma membrane. Any differences in the processes of spermatogenesis can only concern the greater or less development of a cellulose membrane around the spermatids. It may be true that this cellulose membrane is entirely absent in Cycas and Zamia, but if present it would be merely a shell like envelope around the sperm and cannot affect its morphological unity and agreement with the sperms of pteridophytes. A comparative study of the composition and formation of the walls enclosing sperm nuclei in the spermatophytes is much needed to carefully distinguish between plasma membranes and the cellulose secretions that may be developed by them.

While the cycads and Ginko have very much the largest sperms known and are consequently extremely favorable for an examination of spermatogenesis nevertheless some surprisingly detailed studies have been made among the Filicineæ and Equisetineæ. Following his preliminary announcements ('97a, '97b, '97c), Belajeff published in '98 an account of spermatogenesis in Gymnogramme and Equisetum. These forms present histories parallel to each other and to the cycads. Two deeply staining bodies (blepharoplasts) appear on opposite sides of each nucleus previous to the final mitosis in the antheridium which differentiates the spermatids. Consequently each spermatid receives a blepharoplast which lies close beside the nucleus. The blepharoplast begins to elongate and is followed by the nucleus so that both structures form two parallel bands which take a spiral form. (Illustrated in Fig. 3*h* of Section I.) The rest of the cytoplasm remains as a vesicle which comes to lie at the larger end of the sperm. The cilia of Equisetum could be traced to

definite granules in the band as it develops from the compact spherical blepharoplast.

There appeared almost simultaneously with the foregoing contribution of Belajeff a paper by Shaw ('98b) on Onoclea and Marsilia. Shaw investigated the cell divisions preceding the formation of the spermatids in Marsilia and discovered some very interesting conditions. The two blepharoplasts which are found in the mother cell of the spermatid are foreshadowed by smaller bodies which appear at the poles of the spindle in the two previous mitoses. The first of these structures was called a blepharoplastoid. The blepharoplastoid first appears besides the daughter nucleus after the third mitosis previous to the differentiation of the spermatids. There is therefore one for each nucleus of the grandmother cell of the spermatid. This blepharoplastoid divides but the halves remain close together and the pair passes to one side of the cell. With the next mitosis (the second previous to the differentiation of the spermatids) two new structures are formed at the poles of the spindle and from these the blepharoplasts arise. They accompany each daughter nucleus after this mitosis into the mother-cell of the spermatid. Then each divides and the two blepharoplasts pass to opposite sides of the nucleus which prepares for the final mitosis of the series. This division gives a daughter nucleus to each blepharoplast and the spermatid is thus organized. The later history of the spermatid as it changes into the sperm is identical with Belajeff's results.

Belajeff ('99) followed Shaw's account of Marsilia with a study of the same form and came to very different conclusions which have to do chiefly with his belief that the blepharoplast is a centrosome, a view that will presently be considered in connection with the opinions of Strasburger and others. Belajeff found centrosome like bodies (blepharoplastoids of Shaw) at the poles of spindles in various mitoses preceding the formation of the spermatids with their unquestioned blepharoplasts. He is not willing to concede that these centrosome like structures pass into the cytoplasm to disappear there as Shaw states for the blepharoplastoids. He also found the blepharoplasts at the poles of the spindles, which was not observed by Shaw, and holds that they have a part in spindle formation.

We are now prepared to take a general survey of the processes of spermatogenesis to harmonize as much as possible the conflicting opinions respecting the homologies of the blepharoplast. Strasburger (:00, pp. 177–215) has critically reviewed the subject and his conclusions are of great interest. He emphasizes the kinoplasmic character of the blepharoplast, whether it be a differentiated region of the plasma membrane (as he believes for the zoöspores of Cladophora, Œdogonium, etc.) or a special development in the interior of the cytoplasm (pteridophytes and gymnosperms). Strasburger thinks that all kinoplasmic structures, be they centrospheres, centrosomes or blepharoplasts, hold a very close physiological relation to the substance of the nucleolus and that their appearance and size is largely the result of nuclear activities. Accordingly the blepharoplast might occupy the position of a centrosome without being genetically related to that structure, and in fact centrosomes or centrospheres are to be considered more as products of the cells' activities than as self perpetuating permanent organs. There is abundant evidence that the last possibility is the fact in many forms both plants and animals. Since centrosomes are not found at other periods of the life history of gymnosperms and pteridophytes, Strasburger concludes that the blepharoplasts cannot be genetically related (homologous) with such a structure.

Ikeno and Hirase from their earliest writings have considered the blepharoplast to be a centrosome. Ikeno ('98a) held that the blepharoplast corresponded with the middle piece of the animal spermatozoön. Hirase ('94 and '97) although noting for Ginko that the blepharoplasts did not divide and took no part in spindle formation nevertheless called them attractive spheres. The conclusions of Shaw ('98) and Belajeff ('99) for the same type (Marsilia) have just been summarized and present very different points of view. Belajeff believes that the blepharoplast of Marsilia holds the same relation to the poles of the spindles as a centrosome. But Belajeff's conception of the centrosome ('99, p. 204) is that of a morphological and dynamic center which may or may not be easily demonstrated according to the amount of stainable substance present. From these discussions it is

evident that final judgment cannot be passed until certain questions of fact are established by reinvestigations. Shaw and Belajeff cannot both be wholly correct in their observations and interpretations and much depends upon the exactness of future studies upon Marsilia, other pteridophytes, and in the bryophytes. The problems are also related to the processes of zoöspore formation among the thallophytes.

With respect to the bryophytes Ikeno (: 03) has recently published an account of spermatogenesis in *Marchantia polymorpha*. He reports for the mitoses in the antheridium, preliminary to the differentiation of the sperm mother-cells, that a centrosome appears at the side of each nucleus and divides, the two daughter bodies passing to opposite sides of the nucleus and becoming the poles of the spindle. He gives evidence that the daughter centrosomes sometimes divide again when at the poles of the spindle in anaphase. The centrosome cannot be found at the side of the daughter nucleus after the mitosis is completed but it appears when the nucleus is ready for the next division. Ikeno's explanation of the reappearance of the centrosome is unusual. He believes that the centrosome is formed within the interior of each nucleus as a deeply staining body among the linin threads. This body moves to the nuclear membrane and is thrust out into the cytoplasm through a protuberance from the nucleus. It then lies outside of the nucleus and becomes the functioning centrosome, dividing to form two centrosomes that separate to preside over the poles of the spindle. After the final mitoses in the spermatogeneous tissue the centrosomes remain to become the blepharoplasts of the sperms. Each blepharoplast passes to the plasma membrane of its sperm cell and develops two cilia. There is formed at this time another deeply staining body in the cytoplasm considered by Ikeno equivalent to a "Nebenkörper." The nucleus begins to elongate and the "Nebenkörper" takes a position between it and the blepharoplast and in this manner the much attenuated sperm is organized from the mother-cell.

Ikeno considers the blepharoplast of Marchantia to be actually a centrosome as shown by its behavior during mitosis. His account therefore in the main supports Belajeff 's interpretation

of the blepharoplastoids of Shaw which as just described are regarded by the latter author as centrosomes. Both Belajeff and Ikeno are inclined to use the term centrosome with a looseness that is unusual since the first accounts of this structure gave to it a place in the cell which is not strictly followed in these authors' descriptions of spermatogenesis. Ikeno's account of the intranuclear origin of the centrosome is extraordinary. Intranuclear centrosomes have been reported in several animal forms but they do not leave the nucleus in the manner described by Ikeno.

On the whole the writer is more in sympathy with the views of Webber (:01, pp. 70 to 81), Strasburger and Shaw than those of the other authors. Assuming that the observations upon the cycads and Ginko are correct, Webber is certainly justified in emphasizing the striking fact that the blepharoplasts are completely independent of the spindle in the body cell and that they are formed *de novo* at a distance from its nucleus. These are peculiarities which, if established generally throughout spermatogenesis in plants, will remove the processes entirely from the activities of centrosomes in certain thallophytes (*e. g.* Stypocaulon, Dictyota) and in many animal cells. It is certainly to be expected that a centrosome when present will always hold an intimate relation to spindle formation during mitosis. It need not be a permanent organ in cell genesis and an ever increasing number of investigations indicate that it frequently is not. Therefore many authors hold that the centrosome is rather the morphological expression of a dynamic center than a protoplasmic structure with an individuality comparable to the organs of a cell. But these universal characteristics of centrosomes are apparently not present in the blepharoplasts of the gymnosperms nor, according to Shaw, in the pteridophytes (Marsilia). But then the observations of Belajeff and Ikeno are not in accord with those of Shaw and it is possible that studies in zoöspore formation and gametogenesis among the thallophytes may present the subject in new lights.

For as shown in our discussion of the zoöspore it is not clear whether the blepharoplasts in those cells are always derived in the same manner. We have Strasburger's view that the

structures are thickenings of the outer plasma membrane (hautschicht) and opposed to this Timberlake's account for Hydrodictyon in which the blepharoplast is considered as a structure independent of the plasma membrane although lying in contact with it. It must be apparent that the results of Timberlake are in essential agreement with the events of spermatogenesis in the pteridophytes and gymnosperms while those of Strasburger introduce new elements in giving to the plasma membrane the functions of forming a blepharoplast. The process of spore formation in the ascus must also be considered in this connection for in that sporangium a centrosphere associated with each nucleus develops numerous fibrillæ that resemble so much a cluster of cilia as to suggest at once a blepharoplast-like structure, but this centrosphere of course is an important factor in spindle formation during the mitoses in the ascus. Indeed we may well ask for further studies in spermatogenesis and zoöspore formation before we can expect a solution of the problem of the blepharoplast.

Comparisons have been made between the sperms of animals and plants, and some authors (*e. g.* Wilson :00, p. 175, Belajeff '97c) consider the two cells in essential agreement as to structure and development. However these views rest on the assumption that the blepharoplast is truly the homologue of a centrosome. It seems to be established that the locomotor apparatus of the animal spermatozoön is derived chiefly from one or more centrosomes, generally with the co-operation of archoplasm (idiozome, Nebenkern) present in some form near the nucleus. It is true that in plants the locomotor apparatus is derived from kinoplasm which as we pointed out in Sections I and II corresponds closely to the archoplasm of Boveri, but this is very far from implying that structures formed by the archoplasm and kinoplasm respectively need be homologous. Indeed both archoplasm and kinoplasm are distinguished by their physiological activities rather than by their morphological manifestations which are too various to allow of close genetic relationships. Therefore it seems far from established that spermatogenesis in plants is along the same lines as in animals, especially since the weight of evidence at present indicates that the blepharoplast is not a centrosome.

There are numerous problems connected with the physiology of the sperm that bear directly upon its protoplasmic structure. Some of these will be treated in Section IV in connection with processes of fertilization. But at this time it is well to call attention to the intimate association that sometimes exists between the nucleus and blepharoplast. These structures come into actual contact in Cycas and Ginko through a process put forth from the nucleus. It should also be remembered that Timberlake and Dangeard found the blepharoplasts in the zoöspores of Hydrodictyon and in the cells of Polytoma connected with the nucleus by one or two fibers. The nuclear beak that bears the aster in the ascus suggests a similar relationship. These conditions indicate that the activities of locomotion may depend vitally upon the nucleus.

3. The Egg.

The subject of fertilization is reserved for the next section (Section IV) of this series and the present account will deal only with the structure of the unfertilized egg. As the sperm is derived from a motile gamete identical with the zoöspore, so the egg has had a similar origin. We have traced the steps in this evolutionary process among the algæ in a former paper (*Popular Science Monthly*, Feb. 1903, p. 300). The first indication of a differentiation in the sex of primitive gametes is one of size. The male gametes tend to become smaller while the female contains a greatly increased amount of cytoplasm. One of the important factors determining this differentiation is the number of nuclear divisions which take place in the cells that produce respectively eggs or sperms. There are generally a great many more mitoses in antheridia than in oögonia and consequently a given amount of protoplasm must be very much divided to provide each nucleus with its quota of cytoplasm.

The tendency of oögenesis on the contrary is to conserve the protoplasm for relatively few nuclei, provided for several eggs or for a single nucleus in a solitary egg, with the result that the egg cell is generally richly supplied with protoplasm. Such processes result in large cells with a prominent chromatophore or

numerous plastids and not infrequently a considerable amount of food material. The primitive female gametes were provided with cilia like the male, but with their increase in size came a sluggishness of movement which resulted in much shorter periods of motility on the part of these sexual cells. There are some algæ (*Ectocarpus siliculosus*, Cutleria, Aphanochæte) whose motile female gametes come to rest shortly after their escape from the oögonia and are fertilized as quiescent cells by the active sperms. These female gametes at the time of fertilization behave physiologically like eggs although their development shows a morphology identical with the sperm. When such female gametes dispense with cilia entirely they become eggs.

The absence of cilia does away with very much of the complexity which we have just described for sperms. There is no trace of the blepharoplast in the egg and no indication of the activities associated with this structure, so conspicuous in spermatogenesis. The large motile female gametes of such Algæ as Bryopsis, Cutleria, Aphanochæte and certain species of Chlamydomonas and Ectocarpus will probably show some interesting conditions when the details of their cell structure and development are known, for some of these types are likely to throw light on the relation which the blepharoplast bears to other structures in the cell.

The eggs of all plants (Fungi excepted) are believed to be richly stocked with plastids in sharp contrast to the sperms which are entirely destitute of these structures in all groups above the algæ. The plastids in the eggs of Algæ contain the pigments characteristic of the respective groups giving these cells a very rich coloration and sometimes an elaborate internal structure since these plastids or the single chromatophore generally maintain a symmetrical relation to the nucleus. Leucoplasts (see Fig. 11*a*) have been found in the eggs of angiosperms (Schimper, '85) but detailed studies on the cytoplasm of such cells in spermatophytes, pteridophytes and bryophytes are greatly to be desired to determine the history of plastids during the development of these germ cells and at later periods after fertilization.

The distribution of the plastids in the eggs of Algæ may be so general that the entire cell is colored as in Fucus, Volvox and Sphæroplea. Or, the plastids may be largely or wholly withdrawn from some portion of the egg. It is usual for eggs retained within the parent cell (oögonium) to present a colorless area of protoplasm that becomes the point at which the sperm fuses with the egg. Such a hyaline region is called the receptive spot and is generally situated (see Fig. 11*b*) at the side of the egg nearest the pore or opening in the oögonium through which the sperms enter. Excellent illustrations are presented among the Algæ in Vaucheria (Oltmanns, '95), Œdogonium (Pringsheim, '58, Klebahn, '92) and Coleochæte (Pringsheim, '60, Oltmanns, '98). It has been suggested that the receptive spot is related to the clear ciliated end of the ancestral motile gamete and zoöspore but the structures have not been critically compared to determine the precise character of their protoplasmic structure and development. The receptive spot in some forms (Vaucheria, Œdogonium, Fig. 11*b*) lies directly under the opening that is formed in the oögonium and its protoplasm is probably concerned with the fermentative action that destroys the wall at that point.

The red Algæ (Rhodophyceæ) do not have eggs although in their sexual evolution they are at the level of heterogamy. The female gamete (carpogonium with its trichogyne) is a cell homologous with an oögonium and its protoplasmic contents correspond to an egg, but the protoplast never withdraws from the cell wall to lie freely as a naked mass of protoplasm within the structure. But the general agreement of the carpogonium and trichogyne with the oögonium and its neck like extension in Coleochæte seems to determine without doubt the homologies of the former.

There are very few eggs among the fungi that are strictly comparable to those of the Algæ. Monoblepharis (Thaxter '95a) however unquestionably furnishes such an example. But the eggs of the Saprolegniales and Peronosporales are probably in the author's opinion not directly derived from those of Algæ. They are either a peculiar form of sexual cell called the cœnogamete (Davis :00 and :03) or closely related to this structure

which will be given a separate treatment in this section. The cœnogamete is the homologue of a multinucleate gametangium but its evolutionary tendencies seem to be towards such a reduction in the number of nuclei that in the highest expression of its sexual differentiation the female cell contains a single nucleus and has the general form of an egg. But this process of sexual evolution is entirely independent of the well known lines of development in the Algæ (Davis, *Popular Science Monthly*, Feb. 1903). The female sexual cell of the Ascomycetes (called the ascogonium or archicarp) is probably in most forms the homologue of a gametangium. These subjects will be treated in our account of the cœnogamete.

The egg in the archegonium of bryophytes and pteridophytes is generally reported to have a clearer region on the side nearest the neck and this is called the receptive spot. It is reported by Campbell in his investigations on Pilularia ('88), Isœtes ('91), Osmunda ('92a), Marsilia ('92b), and Marattia ('94), by Shaw in Onoclea ('98) by Thom in Aspidium and Adiantum ('99) and by Lyon in Selaginella (:01). The receptive spot is generally believed to be a portion of the egg differentiated to receive the sperm. It is an open question whether this area is morphologically the homologue of the receptive spot in the eggs of algæ and the clear area at the ciliated end of motile gametes and zoöspores. The problem demands a detailed study of the finer protoplasmic structure to determine whether or not it is kinoplasmic in character. The nucleus is generally situated near the center of the egg and the portions of the cell farthest away from the neck of the archegonium contain coarsely granulate protoplasm which is evidently trophoplasmic, *i. e.*, much of its substance is of the nature of food material and the products of metabolism. The leucoplasts would be supposed to lie in this region of the cell but we know nothing of their presence and behavior in the egg of bryophytes and pteridophytes.

The eggs of gymnosperms generally speaking present sharp contrasts to those of pteridophytes. They are very large, probably the largest uninucleate cells in the plant kingdom, and consequently very attractive for cell studies and some of the best work on the events of the maturation and fertilization of plant

eggs has been done on this group (to be treated in Section IV). Passing over earlier investigations that described accurately the general structure of the egg of gymnosperms we shall consider the results of a number of comparatively recent papers that treat especially the pine, spruce (Picea), hemlock (Tsuga), fir (Abies), cycads, Ginko, Gnetum, Taxodium, etc.

Oögenesis and fertilization in the pine has been the subject of several extensive studies the chief being papers by Dixon ('94), Blackman ('98), Chamberlain ('99) and Ferguson (:01b). The protoplasm of the egg is at first vacuolate but later takes on a denser structure which becomes very puzzling because of numer-

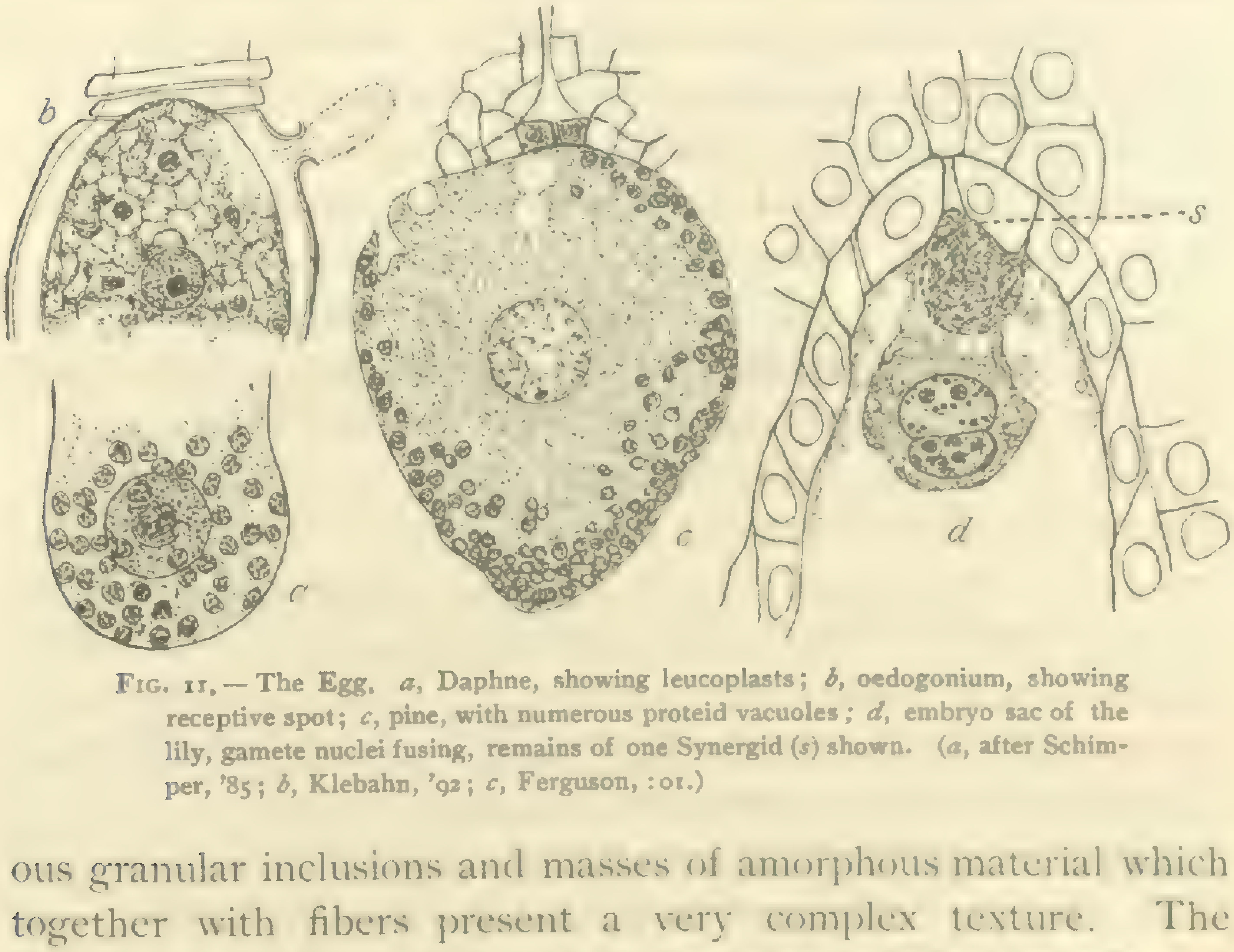

Fig. 11. — The Egg. *a*, Daphne, showing leucoplasts; *b*, oedogonium, showing receptive spot; *c*, pine, with numerous proteid vacuoles; *d*, embryo sac of the lily, gamete nuclei fusing, remains of one Synergid (*s*) shown. (*a*, after Schimper, '85; *b*, Klebahn, '92; *c*, Ferguson, :01.)

ous granular inclusions and masses of amorphous material which together with fibers present a very complex texture. The fibers are sometimes collected in fascicles and they may form a sort of weft at the periphery of the egg or radiate out from the nucleus which is generally surrounded by a kinoplasmic sheath. The complexity is greatly increased as the egg grows older by the development of remarkable structures called proteid vacuoles (See Fig. 11*c*) which have been especially described by Blackman and Ferguson. The number of proteid vacuoles is exceedingly variable in the egg but they sometimes fill three fourths of the structure. They are spaces in the cytoplasmic reticulum filled

with granules and irregular masses of a proteid nature some of which stain like nucleoli. The proteid vacuolee were considered nuclei by earlier writers (Hofmeister and Goroschankin) and recently this view has been revived by Arnold (:00b) who describes the migration of large numbers of nuclei from the cells of the jacket surrounding the egg into that structure. These results have not been confirmed by Ferguson who agrees with the interpretation of other writers that the resemblance of the proteid vacuoles to nuclei is superficial. Miss Ferguson believes that the material of the proteid vacuoles is derived in part from the nucleoli in the cells of the jacket and from those in the egg. A vacuole is reported (Ferguson) at the end of the egg nearest the neck of the archegonium and this is regarded as a sort of receptive spot since the pollen tube discharges its contents into this cavity. The egg nucleus is very large and its contents are not arranged with the regularity generally present in resting nuclei. There are numerous bodies which Chamberlain believes to be chromatic in composition that look very much like nucleoli and have been so designated by that writer. But there is generally one large unquestioned nucleolus and besides this many smaller nucleoli are reported by Ferguson as held in the linin reticulum. Then portions of the linin frequently take irregular forms and stain heavily. There is also present besides the linin, chromatin and nucleoli much granular material (metaplasm), especially in the nuclei of younger eggs, which probably holds some relation to the chromatin although it may readily be distinguished at certain times from that substance.

Recent accounts of the spruce and fir, by Miyake (:03a and :03b) describe conditions very much as in the pine. The egg of the spruce (Picea) is apparently not so fibrous in structure but proteid vacuoles give it a coarse granular structure. He finds no evidence in support of Arnoldi's (:00b) peculiar views that the proteid vacuoles are derived from nuclei that have passed into the egg from cells of the sheath. They are simply masses of nutritive material. There is some doubt whether the vacuoles present at the end of the egg really represent a differentiated receptive spot. The egg of the fir (Abies) conforms in all essentials to the structure in the pine and spruce. There are numerous proteid vacuoles.

It is probable that the eggs of other conifers will be found to present much the same protoplasmic structure and activities as those of the pine. Thus Murrill (:00) describes for the hemlock spruce (Tsuga) a vacuolar receptive spot and figures masses of food material very much like the proteid vacuoles. The general features of the egg of Cephalotaxus (Arnoldi, :00a), Thuja (Land, :02), Podocarpus (Coker, :02), Taxodium (Coker, '03) have been recently described and those of Abies, Larix and Taxus are familiar from older writers but the pine remains as the type of conifer in which the events of oögenesis are best known as regards the details of protoplasmic activities.

Besides the pine we have had some very complete investigations on cycads and Ginko (Hirase, '98, Ikeno, '98b and :01, Webber, :01). In some respects these types and especially the cycads seem to be the most favorable of all the gymnosperms for the study of gametes and the processes of fertilization (to be described in Section IV). The cytoplasm of the egg is comparatively homogeneous in structure so that the cell is relieved from the complicated fibrous structure and proteid vacuoles present in the pine. Ikeno ('98b) finds that the egg of Cycas develops a crater like depression just before and at the time of the fusion of the sperm thus presenting a rather highly specialized receptive spot.

We know almost nothing of the detailed structure of the egg in the Gnetales. Ephedra (Strasburger, '72) develops archegonia much like those of other gymnosperms and we should not expect their eggs to be materially different even in details. But the conditions in Tumboa (Welwitschia) are peculiar and approach more closely those of angiosperms where the egg nucleus is scarcely differentiated from neighboring nuclei lying freely in the protoplasm at one end of the embryo sac. The eggs of Tumboa (Strasburger, '72) are merely cells of the prothallus that push out small projections to meet the pollen tubes. Gnetum presents a further simplification or reduction since the female nuclei lie freely in the protoplasm at one end of the embryo sac. In *Gnetum gnemon* the lower half of the embryo sac is filled with a tissue (Lotsy '99) but in several other species studied by Karsten ('92, '93) no cell walls are found in the entire sac until after fertilization.

The angiosperms present no especial advance over Gnetum in the organization of the egg except that this structure is generally reduced to a single female nucleus and the cytoplasm immediately around it (see Fig. 11 *d*). This egg nucleus flanked by two companions (synergids) and the accompanying protoplasm compose the egg apparatus whose morphology is still a matter of dispute. It is possible that the synergids may stand for portions of a reduced archegonium, but the two nuclei bear such close relations to the egg and polar nucleus that it seems very probable that they are homologous with these structures which have clearly defined sexual potentialities.. In spite of the numerous studies on embryo sacs in various groups of angiosperms we do not yet know precisely how the cytoplasm becomes gathered around the egg nucleus and the synergids. The spindles that are formed between these nuclei in some types (*e. g.*, Lilium) have been supposed to lay down walls by means of cell plates. But there are other forms in which the protoplasm seems to separate along planes of vacuoles without relation to spindle fibers.

(*To be continued.*)

NOTES AND LITERATURE.

ZOÖLOGY.

Dodge's General Zoölogy.[1] — The title on the cover and the "book notice" sent out by the publishers do not suggest that this is otherwise than an entirely *new* book, but in small type on the title page is the information that this is a "revision and rearrangement" of Orton's *Comparative Zoölogy* — a well-known text-book written in 1876 by the late Professor Orton of Vassar College and revised by Birge in 1883 and by Dodge in 1894. But even the information on the title page does not prevent the reader from expecting to find that the new author and new title mean that the book has been recast so completely that the original author deserves credit for only a minor part of the book. Careful examination leads to disappointment. Parts I and II of the original work and its revisions are interchanged, and there are two new chapters — one on practical work and the other on origin of animal species. In all other respects, the chapters, sections, and paragraphs of the greater part of the book stand essentially unchanged, except in minor verbal changes and revisions of the classification and morphology in accordance with discoveries made since the original book and its earlier revisions appeared. Thus Dodge's *General Zoölogy* is analyzed into Orton's *Comparative Zoölogy* with probably 90 per cent of the sentences essentially as Professor Orton wrote them thirty years ago, and added to this about forty pages of new material. In the light of these facts any fair-minded man of science will not hesitate to condemn the change of title and author's credit and especially the method of advertising the book as a *new* one. In all fairness to purchasers and to the principle of credit for original work, the so-called Dodge's *General Zoölogy* should hereafter be known to teachers of zoölogy as Orton's *Zoölogy* revised and extended by Dodge; and as such the chief value of the book is that of the original work with the changes made necessary by advances in zoölogical knowledge. These have been great, but in such a general text-book the majority of the revisions have been possible without rewriting the original sentences.

M. A. Bigelow.

[1] Dodge, C. W. *General Zoölogy*. New York, American Book Co. 1903. 8vo, pp. 512, 379 figs.

Coues' Key to North American Birds[1] had nominally four editions, but the third and fourth were practically reprints of the second (1884) edition. At his death, Dr. Coues was at work on a new edition, the MS. of which was fortunately completed by him. It has been published as the fifth edition of the Key under the direction of Mr. J. A. Farley, to whose conscientious care the publishers give due praise.

The present edition appears in two large volumes containing over eleven hundred pages. The Historical Preface of former editions is followed by a short memoir of the author, being the address delivered by D. G. Elliot at the A. O. U. Congress in 1900. Part I, on Field Ornithology is reprinted without change. Part II on the Structure and Classification of Birds has been somewhat revised. That Dr. Coues nailed his colors to the mast is evident from a paragraph on p. 80, where though he avows his allegiance to the A. O. U. code of nomenclature, he expressly excepts the canon which requires him to misspell a name " for no other reason than because it was misspelled in the beginning."

A less gratifying evidence of his courage in his convictions is given in the discussion of color-change without moult, or Aptosochromatism (p. 92) as Dr. Coues was proud to have termed it. It seems strange that the pages that follow could have been written after the publication of Mr. J. A. Allen's paper in the Bull. Amer. Nat. Hist. 1896.

The chief additions in this edition are in Part III, Systematic Synopsis of North American Birds. Here have been incorporated the results which the study of systematic ornithology has achieved within the last twenty years. The descriptions of many species, and of their nesting habits have been rewritten, particularly in the case of western birds. Many new species and sub-species have been accorded recognition. Such difficult groups as the Small Flycatchers (Empidonax) and the Horned Larks (Otocorys) now appear as they were left by the more conservative treatment of Brewster and Dwight. Most of the changes in nomenclature made by the A. O. U. committee have been accepted, and in some cases some of those not made at the time of Dr. Coues's death were foreseen and included. The changes made since his death appear in an appendix. There have been added to many of the biographies, especially to those of the less familiar birds, the more important synonyms and bibliographical

[1] *Key to North American Birds.* The Fifth Edition. Coues, Elliott, Boston, Dana Estes and Co. 1903. pp. 1152.

references. The accounts of the orders and families have been largely rewritten, and include references to extra-limital groups so that the relationships of North American birds to foreign groups is more clearly brought out. Most of the old illustrations have been retained, and over two hundred new ones have been prepared for this edition by Fuertes. Old admirers of the Key will probably rejoice to see the old familiar cuts, absurdly inadequate or useless as many of them were, and now cruelly contrasted with Fuertes' brilliant work.

The great influence which Coues' Key exercised on the ornithologists of the past generation is well known, and it is gratifying to see his work brought as nearly as possible up to date, and its capacity for usefulness thus prolonged. It was always a bulky book, and now, in its present form, it cannot serve as a manual; it must yield the field to later excellent "Keys." But it may still rank as one of the most valuable works on the reference shelf, especially to those who grew up with it.

One is curious, however, with regard to this work of Fuertes, to know whether it represents that artist's earlier or later style. In some of it his worst faults in bird portraiture are too prominent. In his drawing of the Mountain Chickadee (p. 271) in his efforts to show the plumpness of a vigorous bird, the artist has given us an absurd little caricature.

R. H.

Boulenger on the Classification of Bony Fishes.—The most important recent contribution to the taxonomy of fishes is "A Synopsis of the Suborders and Families of Teleostean Fishes," by Dr. G. A. Boulenger of the British Museum, published in the *Annals and Magazine of Natural History* for March, 1904. It is based on his own studies of the fish skeletons in the British Museum and on the work of Woodward, Gill, Jordan, Starks and Regan. The special effort has been to show the relation of the different members of this great group of nearly 12,000 species by a classification based on our knowledge of phylogeny. The result of Dr. Boulenger's work is not essentially different in fact from that of Dr. Gill, although there is considerable divergence in nomenclature. Dr. Gill has preferred to isolate aberrant groups until their true relationship is known. As a result he has recognized twice as many families and twice as many orders as Boulenger, many of these families and orders being provisional. The advantage of this method lies in clear definition. The

result of leaving aberrant forms in the group nearest to them is to destroy all possibility of exact limitation. It is at the best impossible to frame exact definitions when transitional groups of all grades exist. A few orders can be isolated and defined among the bony fishes, but the group as a whole cannot be divided into orders or suborders or any other categories which shall have even approximately equal value.

There is no sharp line separating the Isospondyli or Salmon-herring series from the Ganoids, from which they are derived. From the Isospondyli or Malacopterygii, as Dr. Boulenger calls them, all other bony fishes seem to be descended. But the line between the Isospondyli and the Haplomi is a narrow one. The Haplomi have lost the mesocoracoid bone, and as it is abortive in many species (Synodontidae, Myctophidæ) hitherto attached to the Isospondyli, these are placed by Boulenger among the Haplomi. Among the Haplomi, on the other hand, are placed the spiny-rayed Percopsidæ because these have not lost the air duct characteristic of the Isospondyli and their allies.

The eels are divided into two suborders, —the Ostariophysi remain together as one. The Heteromi are made to include Dercetidæ, Halosauridæ and Fierasferidæ.

The transitional types with abdominal ventrals, the air duct and the mesocoracoid being lost, constitute two suborders, which do not differ from each other in definition although comprising different categories of families. The first of these is the suborder of Catosteomi, comprising the Selenichthyes (Lampris), the Hemibranchii, the Lophobranchii, and the Hypostomides. The present reviewer sees no reason for associating Lampris with this group. Its suborder (Selenichthyes) is worthy of independent recognition. The others certainly belong together, and almost as certainly are degenerate or specialized allies of the other transitional group of Percesoces.

In Boulenger's scheme, the Percesoces include not only the Atherinidæ-Sphyrænidæ-Mugilidæ series, but also the Scombresocidæ, the Polynemidæ, the Chiasmodontidæ, the Tetragonuridæ, the Stromateidæ, the Ophiocephalidæ, and the Anabantidæ. As thus arranged, the group is defined only by the imperfect attachment of the ventral fins to the thoracic arch. It cannot be exactly defined and its members are very divergent. It is fair to say, however, that the fault lies with the fishes, not with the classifier. The transitional elements between soft-rayed and spiny-rayed fishes are all still extant, and their intergradations defy classification. For this reason, Dr. Gill once

proposed the name Teleocephali for the order containing the whole ancestral trunk of the bony fishes, from the primitive semi-ganoid types to the highly specialized cottoids and labroïds, leaving only the divergent branches to be recognized as separate orders.

The Anacanthini, relieved of the flounders which have no relationship to the cod-fishes, Dr. Boulenger places near the Persesoces.

The Ammodytidae are wrongly placed by Dr. Boulenger with the Percesoces; as in Embolichthys, the genus possessing ventral fins, has these fins at the throat.

The great body of the remaining fishes are placed in the suborder Acanthopterygii, defined essentially as by Gill, Jordan and Evermann and Hay. The Beryces are placed among the Perciformes. The recent discovery by Mr. Starks that all Beryces possess the orbitosphenoid bone, absent in other Acanthopterygii and characteristic of the lower forms, indicates that the Beryciformes (Pempheris and Aphredoderus excluded) should form a division by themselves.

The group Zeorhombi, containing Zeidæ and the flounders, represents an ingenious guess. Even if the flounders, as is probable, be descended from ancestors of Zeus, the present differences justify their separation into a distinct division. Zeorhombi is insusceptible of definition. The remaining orders, Opisthomi, Pediculati, Plectognathi, are arranged as generally accepted, but the Plectognathi are only specialized and degraded offshoots from the Chætodontidæ–Acanthuridæ series with which they form a nearly continuous line of degeneration.

As Dr. Boulenger extends the range of his work, he will find it convenient to recognize a greater number of families, while American ichthyologists will mark their progress by the gradual reduction of the number defined by them. This arises from a different method of work, a different view as to convenience in regard to divergent or imperfectly known forms. Thus every year brings workers on the taxonomy of fishes nearer and nearer together, and farther and farther from the Cuviernian idea of the perch as a perfect fish to be placed first with the others following after.

D. S. J.

Notes on Recent Fish Literature.— In the *Bulletin U. S. Fish Commission* (1902) Jordan and Evermann describe two new fishes from Hawaii, *Tropidichthys psegma* and *Iracundus signifer*, the latter representing a new genus of Scorpænidæ, allied to Pontinus.

In the *Bulletin of the U. S. Fish Commission* for 1902 (1903),

William C. Kendall gives a useful list of the certain river-fishes of Maine. *Leuciscus carletoni*, a new species, with a barbel, and therefore better referred to Couesius, is described as also *Pimephales anuli* (named for Edgar E. Ring) and *Coregonus stanleyi*.

In the *Revista Chilena de Historia Natural* (Valparaiso, VII, 1903) Dr. F. T. Delfin discusses in much detail the fishes known as Congrios in Chile, Ophidiidæ of the genus Genypterus.

In the *Smithsonian Miscellaneous Collections* (XLV, 1903), Dr. C. H. Eigenmann defines 21 new genera of South American river fishes of the group of Characinidæ in advance of his monographic review of the group. It is to be regretted that a closer adherence to classical models did not prevent the suggestion of such names as Holoshesthes, Stichonodon, Colossoma and Mylossoma.

In the *Proceedings of the Zoological Society* of London (1903), Mr. C. T. Regan gives a review of the East Indian fishes of the genus Triacanthus. In this as in many other cases it appears that the species recognized by Dr. Bleeker are all really valid in spite of the doubts expressed by subsequent authors with more scanty material.

In the *Proc. U. S. Nat. Museum* (XXVI), Barton A. Bean describes a new minnow, *Notropis brimleyi* (near *N. coccogenis*) from Cane River, North Carolina.

In the *Atti della Società Italiana di Scienze Naturali* (XLII, 1903), Dr. Cristoforo Bellotti of the Museum of Milan describes an interesting new species of fish, *Pteraclis macropus*, taken off Yokohama.

In the *Proceedings of the U. S. National Museum* (XXVII, 1904), Mr. E. C. Starks discusses the osteology of the berycoid fishes. This group is one of especial interest because it appears earlier in geological time than any other of the distinctly spiny-rayed types, and it is probable that all these are described from Berycoid stock.

Dr. Boulenger unites the berycoids with his perciformes, notwithstanding the archaic characters retained by most of them. Mr. Starks shows that all of them retain one hitherto unnoticed archaic character which is lost in all the other spiny-rayed fishes. This is the development of the bone called osbitosphenoid.

This bone he finds in Hoplostethus, Beryx, Holocentrus. Myripristis. Polymixia and Monocentris. It is not found in Pempheris or in Aphredoderus, which genera should be excluded from berycoid association. The orbitosphenoid is present in the Isospondyli and in the ganoids. It is wanting in the Haplomi and in Aulopus and

Synodus. This fact may indicate an additional character by which to distinguish the order Haplomi, and that Boulenger is right in referring Aulopus and Synodus to this order.

Starks finds that the close resemblance of the barbels in Polymixia to those in Mullus and Upeneus has no phylogenetic significance. While the organs in the two cases look much alike, they are developed in quite different fashion.

In Polymixia each barbel is suspended from the hypohyal, where three short, rudimentary branchiostegals curve around its thickened base. In Mullus and its relatives, the barbel is the extreme tip of a slender ray of bone attached to the end of the ceratohyal, and without relation to the branchiostegals.

In the *Bulletin of the U. S. Fish Commission* (1902, published 1904), Professor John O. Snyder gives a list of the shore fishes taken by the "Albatross" expedition in 1902. Two hundred and twenty-seven species are recorded, with excellent figures of 25 new species not taken by the previous expeditions of Dr. O. P. Jenkins (1889) and Jordan and Evermann (1901). Two new genera are described, Veternio, a toothless Conger eel, and Collybus, a genus of Bramidæ.

In the *Bulletin U. S. Fish Commission* (for 1902, published in 1904), Dr. Jordan gives a list of species of small fishes from coral pools, taken at the Tortugas, Florida, by Dr. Joseph C. Thompson, U. S. N., now surgeon of the "Albatross,"—*Ctenogobius tortugæ*, *Gnatholepis thompsoni*, *Elacatinus oceanops*, and *Ericteis kalisheræ*. Elacatinus is a new genus of gobies, Ericteis a new genus of blennies, in which group another genus, *Acteis* (*moorei*), is detached from Malacoctenus.

Chaetodon bricei is shown to be the young of *Chætodon capistratus*, and the nominal species of Doratonatus are all probably identical with *D. megalepis*. The rare *Holocentrus siccifer* (Cope 1871) is again recorded.

Mr. Henry W. Fowler, now of the Academy of Natural Sciences at Philadelphia, has in the *Proceedings* of that institution (1903) a number of papers on fishes largely of the Pacific Ocean. Of special interest are the following: *Atherina sardinella*, a new species from Italy; Atherinomorus, a new sub-genus for the West Indian *Atherina laticeps*. *Protistius semotilus* Cope redescribed. This genus is allied to Atherinopsis, but has only a single dorsal spine. Gastropterus Cope is the same as the later Pisciregia of Abbott.

Atherinops magdalenæ Fowler is described from Magdalena Bay, Lower California. *Mugil kelaarti* is described from Honolulu. *Liza caldwelli* is redescribed from Samoa. A new sub-genus, Aodalechilus, is proposed for *Mugil labeo*. *Sphyræna tome* is described from Sambaia, Brazil. *Centrobranchus chærocephalus* is described from Hawaii. Centrobranchus is a new genus of Myctophidæ allied to Rhinoscopelus, but the gill rakers reduced to bunches of spines.

Numerous species are recorded from Zanzibar. These papers are illustrated with good plates.

In the Danish *Meddelser om Grönland* (XIX, 1904), Mr. A. S. Jensen gives a list of the fishes of Eastern Greenland, based on the collections of the Amdrup-Hartz expedition of 1900. Thirty-six species are included, the following being new: *Lycodes eudipleurostictus*, *Lycodes* (*reticulatus*) *macrocephalus* and *Lycenchelys kolthoffi*. Excellent faunal notes are given with a very convenient bibliography. According to Jensen, the American Cottus or *Oncocottus hexacornis* is identical with the European *quadricornis*, as Jordan and Evermann had suspected. The American *Artediellus atlanticus* is also shown to be the same as the European *A. uncinatus*, from which Jordan and Evermann thought it apparently distinct. The name *Icelus bicornis* is rightly used instead of the later *Icelus hamatus*. The Greenland species known as *Liparis tunicata* proves to be the same as *Liparis liparis*. *Liparis fabricii* is different. *Paralepis kröyeri* is shown to be different from *P. borealis* and the Charr of East Greenland is identified as *Salmo* (better *Salvelinus*) *alpinus*. The engravings are entirely worthy of this admirable piece of faunal study.

Professor Keinosuke Otaki of the Imperial Military Academy of Tokyo, a graduate of Stanford University, has begun in connection with Professor T. Fujita and T. Higurashi the publication of a serial work entitled "Fishes of Japan." The text is in Japanese and English. The species included in part first are *Lateolabrax japonicus*, *Latilus sinensis*, *Gymnosarda affinis* and *Seriola quinqueradiata*. These are illustrated by colored plates well executed by Mr. K. Ito.

In the Report on the Sea and Inland Fishes of Ireland for 1901, Messrs. E. W. L. Holt and L. W. Bryne describe and figure a translucent symmetrical larval flounder, which they regard as the young of the "White Sole," *Glyptocephalus cynoglossus*. The mouth is shown as much larger than in the adult of this species, which may throw doubt on the identification.

The same gentlemen in a later paper describe and figure all the British gobies. Their plates will greatly aid in the identification of these little fishes.

In the *Annuaire du Musèe Zoologique* at St. Petersburg (VIII, 1903), L. S. Berg discusses a collection of Cottoid fishes from Lake Baical, with observations — unfortunately in Russian — on the classification adapted by Jordan, Evermann and Starks. Two new genera, *Baicalocottus* and *Batrachocottus*, are defined, with the genus Procottus of Gratz.

When the present writer was in Japan in 1900, the Imperial Museum generously placed at his disposal all duplicates of new species of fishes contained in the Museum. Those represented by single examples could not be sent away, and these the director of the Department of Natural History, Dr. Chiyomatsu Ishikawa, has undertaken to describe for the sake of completing the rich faunal list of Japan.

In the *Proceedings of the Imperial Museum*, Dr. Ishikawa describes the following new species, most of them with good figures:

Zezera hilgendorfi, *Zacco mitsukurii*, *Leuciscus dorobaë*, *Stromateoides nozawæ*, *Heterognathodon dœderleini*, *Cirrhilabrus lyukyuensis*, *Amphiprion snyderi*, *Crenilabrus stejnegeri*, *Tetraroge kagoshimensis*, *Hemitripterus nipponicus*, *Podothecus tokubire*.

Of these the Crenilabrus from the Riu Kiu Islands is the most interesting, as that genus, largely represented in the Mediterranean, had never before been recorded in other waters. The Tetraroge should rather be referred to the genus Erisphex.

In the *Records of the Australian Museum* (V, 1904) Mr. Edgar R. Waite gives an account of his explorations of Lord Howe Island. Seventeen known species of fishes were added to the fauna of this interesting island. Ten new species were discovered, most of these with a number of other interesting forms being figured by Mr. Waite. The new genera are Xenogramma (Gempylidæ), Allogobius, Limnichthys (Trichonotidæ) and Lepadichthys (Gobiesocidæ). The fauna as a whole, although distinctly tropical, is very different from that of Hawaii or Samoa.

In the same *Records* (V, 1904) Mr. Waite gives a list of the fishes known from Lord Howe Island, 180 in number, with a bibliography. The list is especially useful for comparison with faunal lists of the South Seas, the genera being largely identical, the species different. In this list Mr. Waite has taken special care to verify the dates of publications.

In the *Transactions of the American Philosophical Society* (XX, 1901) Dr. O. P. Hay gives a valuable table showing the chronological distribution of the genera of elasmobranchs. He calls attention to one remarkable fact. While many genera and species (Cladoselachidæ, Acanthoëssidæ, Psammodontidæ, Pleuracanthidæ, Cladodontidæ, etc.) occur in the Devonian and Carboniferous ages, only three genera remain in the Permian and but four in the Triassic. All these are Heterodontidæ, the successors or descendants of the Orodontidæ of the Carboniferous. In the Jurassic, numerous families with many genera appear, and through these from Heterodontid stock the modern sharks seem to have sprung. Apparently the Paleozoic families, except the Orodontidæ, have no modern descendants.

In the *Bulletin of the Museum of Comparative Zoölogy* (XLI, 1904) Samuel Garman gives an elaborate and excellent account with beautiful plates of the anatomy of the long-nosed Chimæra of Japan, *Rhinochimæra pacifica* (Mitsukuri). In connection with the study of this species, he has given a general account of the living chimæroid fishes, with figures of some of them. On grounds of priority, Mr. Garman substitutes the name Chismopnea Rafinesque, 1815, for the later name Holocephala of Muller (1834).

In the *Geological Magazine* (IX, 1902) Dr. Charles R. Eastman founds a new family of fossil sharks, Peripristidæ, on the genus Peripristis (Pristodus).

In the *American Geologist* (XXX, 1902) Dr. Bashford Dean gives illustration of a startlingly perfect preservation of the muscular fibre of a shark, *Cladoselache fyleri*, in the Cleveland shales. This was an estuary deposit originally of fine mud, in which the fish remains became phosphatized.

In the *Proceedings of the Academy of Natural Sciences of Philadelphia* (1903) Dr. Carl H. Eigenmann and Clarence H. Kennedy discuss a large collection of river fishes, made in Paraguay by Prof. J. D. Anisits of the Paraguay National University. One hundred and nine species are noted, many of them new, and the paper is followed by a useful biography. A feature of special convenience is a synopsis of the genera of Cichlidæ, 25 in number, Biotodoma and Biotœcus being new names.

In the *Annotationes Zoologicæ Japonenses* of the Imperial University of Tokyo Dr. Bashford Dean gives a study of the development of the egg of the Japanese shark, *Heterodontus japonicus*. He finds good evidence of the existence of holoblastic cleavage.

In the Christiana *Videnskabs-Selskabs Vorkandlinger* for 1902 and 1903 (the last volume being published from the Fridtjof Nansen fund) Dr. Robert Collett gives additional records of additions to the fish fauna of Norway. These admirable notes are of great value to the student of the fishes of Northern Europe, as well as of Northern regions generally.

Jordan and Starks continue in the *Proceedings of the U. S. National Museum* (XXVII, 1904) their monographic accounts of the fishes of Japan.

In the review of the Scorpænidæ 52 species are described as Japanese, 14 of these being new. These are arranged in 23 genera, the following being new: Thysanichthys, Sebastiscus, Lythrichthys, Ebosia, Decterias, Inimicus, Ocosia. Erisphex. The new species and most of the new genera are figured.

The Cottidæ of Japan are also described in detail by the same authors. In these fishes as in the Scorpænidæ, of which the Cottidæ are the Arctic descendants, the waters are particularly rich. Fifty-seven species are described, 19 being new. These are arranged in 40 genera, the new genera being Stlengis, Schmidtia. later called Schmidtina, the name Schmidtia being preoccupied. Daruma, Ricuzenius, Rheopresbe, Ainocottus, Crossias, Elaphichthys, Alcichthys, Furcina, Ocynectes, Bero, Vellitor.

Similar reviews cover the less numerous species of the families of Agonidæ and Hexagrammidæ.

The two species of white Chimæra (*Chimæra phantasma* and *Chimæra mitsukurii*) found in Japanese waters are described and figured by Jordan and Snyder.

D. S. J.

PALÆONTOLOGY.

Eastman's Translation of Zittel, Vol. II.[1]—Since the publication of the first volume of Dr. Eastman's translation of Zittel's *Grundzüge der Palæontologie*, English speaking students have awaited with keen interest the appearance of the second volume. and it may

[1] von Zittel, Karl A. *Text-Book of Palæontology*. Vol. II. Translated and edited by Charles R. Eastman. London and New York, Macmillan. 1902. 8vo, 283 pp., 373 figs.

be said that the latter fully maintains the high standard set in the earlier portion of the work. The present volume treats of the Vertebrates, with the exception of the mammalia, to the consideration of which class the third and last volume will be devoted.

The general method of treatment which has made Zittel's works so valuable to the student happily has been closely adhered to in the translation; we refer especially to the introductory sections on the various classes, and to the brief diagnosis in italics with which the consideration of each group,— class, sub-class, order and family, — is introduced. It is largely to this latter feature that these works owe their superiority as books for ready reference.

In comparing the English edition with the original we note first very considerable amplification and revision, representing the advance in Palæozoölogy during the seven years since the publication of the earlier work, and in this enlargement and revision Dr. Eastman has had the collaboration not only of the author but of a number of competent English and American specialists. As regards Taxonomy the changes from the original have been very slight, far less indeed than we had hoped to see, and it is to be regretted that the editor and his collaborators so far subordinated their own views on classification to those of the author, since some rearrangement, especially of the fishes and reptiles, was quite desirable.

The entire section on fishes has been translated and revised by Dr. Arthur Smith Woodward of the British Museum. Dr. Woodward has been rather conservative in the matter of revision and has kept his own opinions on taxonomic points very much in the background. Of this section the part on ostracoderms has undergone the most extensive revision, chiefly based on the recent researches of Traquair. Thus we find Traquair's order Anaspida included, and in all nine families of ostracoderms are recognized. The Arthrodira, which in the original were given ordinal rank among ostracoderms, are now very properly placed as a sub-class, but the Macropetalichthyds — the Anarthrodira of Dean — are ranked *incertæ sedis*. It is rather to be regretted that the old division of the bony fishes into Ganoidei and Teleostei has been adhered to, instead of the better morphological differentiation of Crossopterygia and Actinopterygia. The old system has, however, the merit of familiarity and convenience. The section on ganoids has been amplified about one half and has been thoroughly revised. Little is said regarding the systematic position of the Dipnoi, but we can scarcely approve of their place in the book, in immediate sequence to the Arthrodires; it suggests tacitly the former supposed relationship of the two groups.

The section on Amphibia, revised by Dr. E. C. Case, differs but little from the original, except in the added descriptions of several genera. The taxonomic system is unaltered and, on the whole, is quite satisfactory, but it must be conceded that the Phyllospondyli of Zittel (the Branchiosauria) do not form a group coördinate with Lepospondyli, and there is much to be said in favor of comprising the Branchiosauria, Microsauria, and Aistopoda as sub-orders of the order Lepospondyli.

The treatment of the reptiles, in which the editor had the collaboration of H. F. Osborn, S. W. Williston, J. B. Hatcher and O. P. Hay, occupies nearly one half of the book, and is admirable in details, such as the descriptions of smaller groups, but the taxonomic arrangement shows nothing of the relationships of the various orders which compose the class. It is regrettable that the revision of this section was completed before the appearance of recent papers by R. Broom, H. F. Osborn and others, which show in a convincing manner that the reptiles have had a diphyletic evolution. Some of these papers have considerably amplified our knowledge of the Anomodontia and have indicated that the Parasuchia constitute an order quite distinct from the Crocodilia.

To Mr. F. A. Lucas is due the credit for the enlargement and thorough revision of the section on birds. This part has been almost entirely re-written, and a different taxonomic scheme, based chiefly on Stejneger's classification, has been adopted, to the marked improvement of the book, although, as Mr. Lucas explains, it is not possible in the case of birds to do more than group related forms, and quite out of the question to arrange the groups so as to indicate phyletic relationships.

It will be noted that the points here criticised are all points of classification, points on which the editor and his collaborators were not entirely free to express their personal views. The translation and revision have been excellently done, and we may say that Dr. Eastman has given us in the present volume the most useful text-book published on the Palæontology of the verebrates below mammals. We trust that the volume on mammals may be as good.

J. H. McG.

BOTANY.

A New Book on Ferns.[1] — For all who study or wish to study our native ferns, Dr. Waters has prepared a book which is sure to prove both helpful and inspiring. The numerous photographic illustrations include enlarged views of the fructification in which the generic characteristics are often surprisingly well brought out. Specific and varietal differences which frequently prove perplexing to beginners are clearly shown in photographs of fronds or entire plants. Sometimes these are grouped instructively in series to exhibit the range of variation. Especially charming and significant are the views showing typical habits and habitats.

The text besides pointing out the features by which forms are discriminated, directs attention most happily to the out-door aspects of ferns — their adaptations and preferences — in a way to encourage the best sort of field work. As a help to determining specimens not in fruit the key based upon characters drawn from the stipes will doubtless prove welcome to all students of the group. While exception might be taken to such unnecessary departures from botanical accuracy as the use of "stem" for stalk or stipe, the substitution of untechnical for technical expressions has been, on the whole, skillfully done. Dr. Waters writes as a lover of ferns and his contagious enthusiasm suffuses the whole book.

F. L. S.

Porter's Flora of Pennsylvania.[2] — For sixty-five years Professor Porter was an assiduous and intelligent collector and student of the flora of the State in which he lived. A contemporary of Darlington, Torrey and Gray, he shared their knowledge and views; but he lived to see a school of natural grouping of orders, species segregation, and nomenclatorial reform, quite different from theirs, come to the front, and the editor of this posthumous Flora tells us that being thoroughly acquainted with the author's ideas he can confidently say

[1] Waters, Campbell E., Ph. D. *Ferns*: A manual for the Northeastern States, with Analytical Keys based on the Stalks and on the Fructification, and over 200 Illustrations from Original Drawings and Photographs. New York, Henry Holt & Co. 1903. 4to, xii + 362 pp.

[2] Porter, J. N. *Flora of Pennsylvania.* Edited, with the addition of analytical keys, by J. K. Small. Boston. Ginn & Co., 1903. 8vo, pp. xv + 362, with outline map.

that he would have heartily subscribed to everything in it as published. The book is essentially a list of the spermatophytes or flowering plants of the State, arranged in the phylogenetic sequence of Engler and Prantl, with keys to the orders, families, genera and species, and copious indexes to Latin and vernacular names. The nomenclature adopted is apparently based on the Rochester code, a common name is given for each species, with a reference to its description in Britton's *Manual*, and its figure, if one is published, in Britton and Brown's *Flora*,— to supplement the terse characters embodied in the keys; and each is accompanied by a brief indication of habitat, general geographic distribution, and an enumeration of the counties in which it occurs in Pennsylvania. As a determination hand-book, it is one of the best local floras thus far published. Its defect — if it be one — lies in the omission of all synonymy, leaving a very large proportion of the plants under names different from those by which they were known to the author during the greater part of his life and by which his contemporaries referred to them in their classic publications, and without intimation to the novice that this is the case or direct indication of any means by which the two may be correlated,— the Manual referred to being of no assistance in this matter.

W. T.

The Journals.— *Botanical Gazette*, February: — Darwin, "On a Self-recording Method applied to the Movements of Stomata"; Holferty, "The Archegonium of *Mnium cuspidatum*"; Lewis, "Studies of some Anomalous Dicotyledonous Plants"; Shriner and Copeland, "Deforestation and Creek Flora about Monroe, Wis."; Snow, "The Effects of External Agents on the Production of Root Hairs"; Duvel, "Preservation of Seeds Buried in the Soil"; MacMillan, "Cumaphytism in Alaria."

Botanical Gazette, March: — Garber, "The Life History of *Ricciocarpus natans*"; Merriman, "Vegetative Cell Division in Allium"; Smith, "Undescribed Plants from Guatemala and other Central American Republics — XXV"; Thom, "*Craterellus taxophilus* a New Species of Thelephoraceæ"; Greenman, "Notes on Southwestern and Mexican Plants."

Botanical Gazette, April: — Bennett, "Are Roots Aerobic?"; Nelson, "Contributions from the Rocky Mountain Herbarium — V"; Lyon, "The Evolution of the Sex Organs of Plants";

Robertson, "The Structure of the Flowers and the Mode of Pollination of the Primitive Angiosperms"; Coville, "Arcterica, the Rarest Genus of Heathers"; Ganong, "New Precision-Appliances for Use in Plant Physiology."

The *Bryologist*, March: — Fink, "Further Notes on Cladonias — *Cladonia fimbriata*"; Holzinger, "The Genus Anacolia in North America"; Cardot, "Notes on Some North American Mosses"; Collins, "Some Erroneous References"; Grout, "A New Brachythecium — *B. rivulare tenue*"; Towle and Gilbert; "The Fruiting Season of the Hair-cap Moss."

Bulletin of the Torrey Botanical Club, March: — Arthur, "Taxonomic Importance of the Spermogonium"; Harshberger, "A Phyto-Geographic Sketch of Extreme Southeastern Pennsylvania"; Cushman, "Desmids from Southwestern Colorado"; Britton, "Four new North American Birches"; and Richards and MacDougal, "The Influence of Carbon Monoxide and other Gases upon Plants, — a Correction."

The *Fern Bulletin*, January: — Parish, "The Fern Flora of California"; Clute, "Measurement of Variation in Equisetum"; Hill, "Remarks on some Fernworts of Western New York"; Clute, "A New Species of Equisetum [*E. Ferrissi*]"; Eaton, "The Genus Equisetum in North America — XVI"; Klugh, "Treasure Trove"; Fetherolf, "*Asplenium ebenoides*"; and a biographic sketch, with portrait, of Sarah Frances Price.

Journal of the New York Botanical Garden, April: — Anderson, "Protection of our Native Plants"; Rusby, "Beverages of Vegetable Origin"; and Howe, "The Pike Collection of Algæ."

Ohio Naturalist, February: — Kellerman, "Index to Uredineous Culture Experiments, with List of Species and Hosts for North America"; Schaffner, "Some Morphological Peculiarities of the Nymphaeaceæ and Heliobiæ.

Ohio Naturalist, March: — Schaffner, "Ohio Plants with Extra-Floral Nectaries and other Glands."

Ohio Naturalist, April: — Cook, "Galls and Insects producing them, with Appendix."

The *Plant World*, February: — Safford, "Extracts from the Note-Book of a Naturalist on the Island of Guam — XV"; Price, "Kentucky Oaks"; Safford, "Henry Elwood Baum (with portrait)";

Squires, "Wild Flowers of Prairie and Canyon in Northern Idaho"; Beal, "What is a Bud and how long does it retain its Identity"; Pepoon, "Destruction of a Farm Flora."

The *Plant World*, March: — Safford, "Extracts from the Note-Book of a Naturalist on the Island of Guam — XVI"; Waters, "Plant Wounds and Natural Pruning"; Blodgett, "Frost-Weeds and other Winter Notes"; Bailey, "Undraped Trees"; Britton, "Relations of Plants to Birds and Insects."

Rhodora, February: — Davenport, "Recollections of Charles Christopher Frost (with portrait)"; Ames, "*Spiranthes neglecta*"; Davenport, "Miscellaneous Notes on New England Ferns — VI"; Fernald, "Preliminary Lists of New England Plants — XIII. Juncaceæ"; Collins, "The Black Spruce in Rhode Island"; Weatherby, "*Panicum Commonsianum* in Connecticut"; Andrews, "Some Interesting Mosses from a Southern Vermont Peat-Bog"; and Ames, "*Spiranthes Grayi.*"

Rhodora, March: — Leavitt, "Partial Reversion in Leaves of the Fern-leaved Beech"; Graves, "Noteworthy Plants of Southeastern Connecticut"; Robinson, "Identity of *Anychia dichotoma*"; Rehder, Preliminary Lists of New England Plants — XIV."

Rhodora, April: — Chase, "North American Allies of *Scirpus lacustris*"; Andrews, "Bryophytes of the Mt. Greylock Region — III"; Slosson, "A New Hybrid Fern from Vermont"; Sanford, "The Range of *Saururus cernuus* extended into R. I."; Harger, "Some Introduced Plants of Ct."; Nye, "Bulblets of *Microstylis ophioglossoides*"; Knight, "*Cleome serrulata* in Me."; Graves, "*Helenium nudiflorum* in Groton, Ct."; and Osmun, "Further Stations for *Botrychium matricariæfolium* in Ct."

Torreya, February: — Stone, "Physiological Appliances — II"; Arthur, "An interesting unpublished Work on Fungi"; Britton, Juncaceæ of the West Indies"; Britton, "*Agdestis Clematidea*"; Harper, "New Station for *Arabis Georgiana*"; Burnham, "Notes on *Epigæa repens*"; and Atkinson, "A New Lemanea from Newfoundland.

Torreya, March: — Osmun, "A Summer in Salisbury, Ct."; Sumstine, "The Slime-Mounds of Pennsylvania"; Eggleston, "The Cratægi of Ft. Frederick, Crown Point, N. Y."; Britton, "*Cratægus Porteri.*"

W. T.

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BY

EDWARD L. NICHOLS
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VOL. XXXVIII, NO. 453. SEPTEMBER, 1904

THE AMERICAN NATURALIST

A MONTHLY JOURNAL
DEVOTED TO THE NATURAL SCIENCES
IN THEIR WIDEST SENSE

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THE

AMERICAN NATURALIST.

Vol. XXXVIII. *September, 1904.* No. 453.

SOME OBSERVATIONS ON RORQUALS OFF SOUTHERN NEWFOUNDLAND.

GLOVER M. ALLEN.

Until very recently it has been the usage, in books on natural history, to picture Cetacea, when in their native element, as floating lightly on the surface of the water and sending forth from the blow-holes great columns of spray which break and fall in showers over the back. In the works of the older writers, as Bonnaterre and Lacépède, the spouts of whales are represented as solid columns of water, of nearly uniform diameter throughout, which after reaching their maximum height, curve over, either to the front or to the rear, and, breaking slightly, vanish away. Such representations, however, were recognized as entirely inadequate, being merely the conventional vagaries of the artists. K. E. von Baer ('64) seems to have been among the first to attempt an accurate delineation of the whale's spout. He figures a Finback whale in the act of "blowing," the column being a vertical one, expanding very slightly until the maximum height is reached, when it bushes out and gradually becomes dispersed. Henking (:01) also represents in a very diagrammatic way his impression of the form of a Finback whale's

spout. The outline he makes retort-shaped, and the whole is directed slightly backward. Both these authors add that their observations were made in calm weather with a smooth sea.

Not until 1903 have there been published any actual photographs of the larger whales alive and free in the open ocean. The first published photographs of this nature appear in the report on the Cetacea of the Antarctic expedition of the "Belgica." These represent the Humpback whale (*Megaptera nodosa*) and the Sulphur-bottom (*Balænoptera musculus*) in the various positions assumed during their appearance at the surface of the ocean, and were taken by Dr. E. G. Racovitza and Dr. F. A. Cook, in 1898. Only one view is shown of the spout, and this is so indistinct as to be rather unsatisfactory. Later in the year 1903, Dr. F. W. True (:03[a]) published some very excellent photographs of Finback whales (*Balænoptera physalus*) taken from the bow of a whaling steamer off the east coast of Newfoundland. These views show very well the appearance of this whale in its various postures following the spouting, until its final plunge. No photograph of the spout itself was obtained, however, so that it seems worth while to publish a few views of spouting whales obtained by the present writer a few months ago.

Through the courtesy of Mr. Alexander McDougall, manager of the Newfoundland Steam Whaling Company, I had the privilege of visiting the whaling station at Rose-au-Rue, in Placentia Bay, Newfoundland, during the second week of September, 1903. A number of interesting observations were made at this time and a valuable series of photographs was secured, some of which are reproduced here.

Four species of rorquals are taken on the Newfoundland coast: the Humpback (*Megaptera nodosa*), the Sulphur-bottom (*Balænoptera musculus*), the common Finback (*B. physalus*), and the Pollack whale (*B. borealis*) or, as the Norwegians call it, the "Sejhval." True (:03) was the first to record the presence of the last named species on this side of the Atlantic, on the basis of four specimens taken at the Rose-au-Rue station during the season of 1902. The steam whaling industry at Newfoundland is one of recent origin, having been established in 1898. Accord-

ing to the *Morning Chronicle*, of Halifax, N. S., the amount of whale oil produced in Newfoundland for the fiscal year ending June 30, 1902, was valued at $125,287. In addition to the oil which is tried out from the blubber and carcass, an excellent "guano" is prepared from the refuse flesh and the bones are ground up into lime.

The fishery itself is carried on by means of small and staunchly built iron steamers of something over one hundred tons. A cannon-like gun is mounted on a pivot at the bow, and discharges a five-foot harpoon of over 100 pounds weight, which at short range is nearly buried in the body of the whale. A hollow, iron cap filled with blasting powder is screwed to the tip of the harpoon, forming its point. A timed fuse discharges this bomb inside the body of the whale. The harpoon carries a stout cable which is handled by a powerful 5-sheet winch on the steamer's deck.

On September 9th the writer accompanied the whaling steamer "Puma," Captain Christaffersen, on the daily hunt in the lower part of Placentia Bay, and obtained several successful photographs of living whales at close range. A few of these are here reproduced, and illustrate particularly the spout of the Sulphur-bottom whale (*Balænoptera musculus*), no photograph of which has hitherto been published, with the exception of the one by Racovitza.

Both Finback and Sulphur-bottom whales observed on this occasion seemed to go through a regular series of evolutions, and were doubtless feeding. They rose to spout about once in every 12 to 15 seconds with great regularity for perhaps twelve times, after which they dove for a much longer stay of several minutes. The precise length of the longer periods was not accurately determined, but could hardly have been more than 5 or 10 minutes. On rising, the first part of the animal to reach the surface is the top of the head; at the same time it spouts, and a portion of the long back comes into view. The head is then lowered, the body arches slightly and the descent begins. The back comes curving out of the water and down again, till finally the dorsal fin appears. By the time the fin has reached the surface again in its forward and downward move-

ment the entire body has disappeared. The flukes were not thrown out of water by either of the two species seen alive, as has been noted by True and others.

The whale, in diving, leaves a long "slick" on the water at the spot where it went down, and comes up again in regular course several times its length farther on when making a series

FIG. 1.— A sulphur-bottom whale spouting.

of "spouts" or breathings. The distance between successive spouts seemed to be nearly two or three times the length of the whale, *i. e.*, 150 to 200 feet.

When a whale is sighted the steamer is put about to overtake it, but the endeavor seems to be not so much to head it off as to cut in behind so as not to unduly frighten the animal. On overtaking the quarry, the steamer is manœuvered so as to come

to a stop at about the spot where the whale is expected to rise for the next spout. On one occasion a Sulphur-bottom was thus followed for a considerable distance till finally the vessel came to a standstill at about the place where the next appearance of the animal was expected. The distance had been well judged, and the writer, standing with camera ready, was able shortly to perceive the shadowy form rising obliquely under the port bow. As the whale broke water and shot forth a column of vapor, the click of the camera and the crash of the harpoon gun sounded almost at the same instant. The photograph obtained (Fig. 1) shows the Sulphur-bottom with the region of the blow-holes just

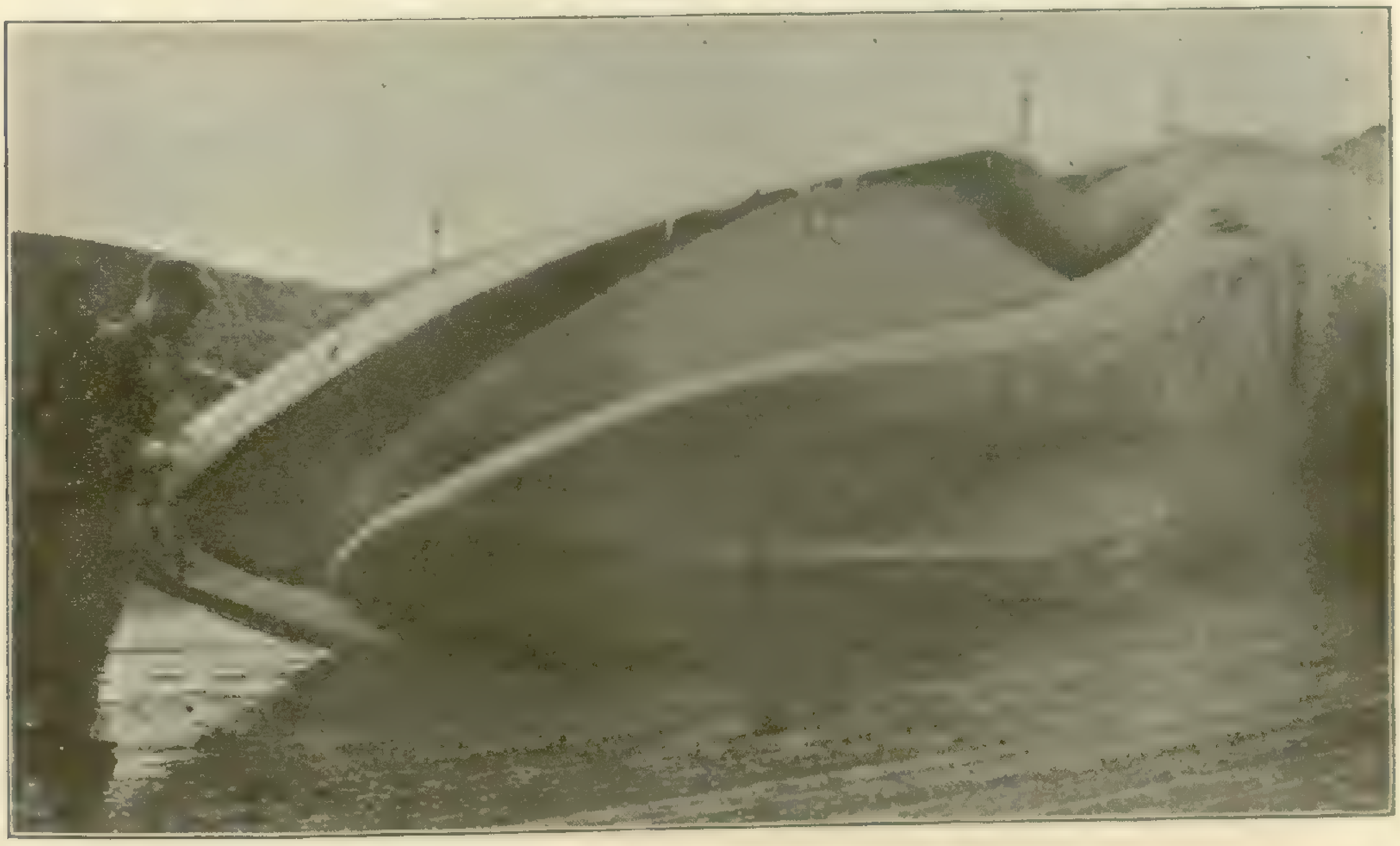

Fig. 2.— Head of a sulphur bottom from above.

out of water. The spout itself was a very short one and is seen to have somewhat the form of a narrow, inverted flask. The wind, blowing from left to right of the picture, carries the upper portion of the vaporous stream away to leeward. The most interesting feature of this view is that the area at each side of the blow-holes is clearly seen to be elevated above the apertures themselves as the breath escapes. The elevation of these ridges is well shown in side view among the photographs obtained by True (:03ª), and in the drawings by Racovitza (:03), but neither of these observers was able to determine satisfactorily whether it was the blow-holes themselves, or only

the adjacent parts, that were thus raised. In the view here shown, which was taken from directly behind the animal's head, there can be no doubt that the portion elevated in spouting is the region lying along the external side of each nasal aperture. The broad, shallow groove or depression extending downward from each side of the blow-holes may possibly be due to the muscular contraction incident to the raising of the two ridges. The same feature in side view is possibly shown in one of the photographs by True (:03, Pl. 25, Fig. 2). No such groove was seen in the dead specimens. The column of vapor itself is clearly single, even though arising from two apertures, for the latter are situated so close together that the two jets

Fig. 3 — Spout of a sulphur-bottom.

of vapor must unite at once. The photographs do not, therefore, bear out Packard's ('66, p. 272) statement, on the testimony of another, that the Sulphur-bottom blows in a "double stream which is directed backward toward the tail." The blowholes of a large whale of this species are represented in Figure 2. The animal lies on its left side with the upper surface of the head toward the observer. The mouth is partly open, and from it projects the fringe of baleen. The two slit-like nasal openings are seen near the lower right hand of the figure and appear to be situated between the arms of a V-shaped prominence whose point is directed forward, and is continued as a slight

median ridge toward the tip of the snout. In the dead animal, however, there is hardly more than this slight suggestion of the nasal ridges which are so prominent in life.

The form of the spout, in both the Sulphur-bottom and the Finback whale, unless distorted by the wind, is that of a simple column, narrow at the base and gradually increasing in diameter with the height, like a jet of steam forced through a small opening. Such a spout is shown fairly well in Figure 1, Plate 1, of Racovitza's (:03) paper. The views obtained by the present writer all show the effect of the light wind blowing at the time, in that the vapor is carried off to leeward to a greater or less

Fig. 4.— An irregular spout of a sulphur-bottom.

extent. Figure 3 shows the spout of a Sulphur-bottom which is fast by a line to the whaling steamer. This view shows the general outline of the column, with a slightly rounded top. Figure 4 shows a spout of an irregular outline from the same whale at closer range. The two harpoon lines by which it is fast to the vessel are seen at the lower right hand. The top of the column is of thin vapor and is being wafted away by the breeze. The lower part of the column is much denser and somewhat in the form of an inverted cone. Possibly the irregular shape may be in part due to a slight wave breaking over the animal's head as it commenced to spout.

The height to which the larger rorquals spout varies consider-

ably according to circumstances. The same individuals are seen at times to make a low spout and again, one twice or perhaps thrice as high. Estimates of the height of the column by seemingly reliable persons run from ten feet up to fifty. It is sometimes stated (*cf.* Beddard, :00, p. 153) that the Sulphur-bottom whale may be recognized by the great height of its spout as compared with that of other large species of rorquals. The writer was unable, however, to distinguish between the spouts of the Finback (*Balænoptera physalus*) and the Sulphur-bottom whale (*Balænoptera musculus*), nor did the men on the whaling

Fig. 5.— Lancing a spouting sulphur-bottom.

vessel believe that the height of the spout afforded any criterion for such a distinction. One of the photographs obtained by the writer, however, affords an opportunity for the direct comparison of the relative heights of a man and of the spout of a whale. Figure 5 shows the captain in the act of lancing a 77-foot Sulphur-bottom which two harpoons had failed to despatch. He stands in the bottom of the boat, alongside the exhausted animal, and the spout, extending up to the skyline in the photograph, is one of average height. The standing height of the man is about

5 feet 8 inches, and the height of the spout is $2\frac{1}{3}$ times as great, or about 14 feet. A maximum spout would probably be close to 20 feet high, which is the estimate I find in my notes taken at the time.

I had no means of accurately estimating the speed at which these whales travel through the water, but it not infrequently happens that the whaler, steaming at ten knots an hour, is unable to overtake a free whale even after a considerable chase. Beddard's statement that the maximum speed of a Sulphur-bottom whale is in the neighborhood of twelve miles an hour is

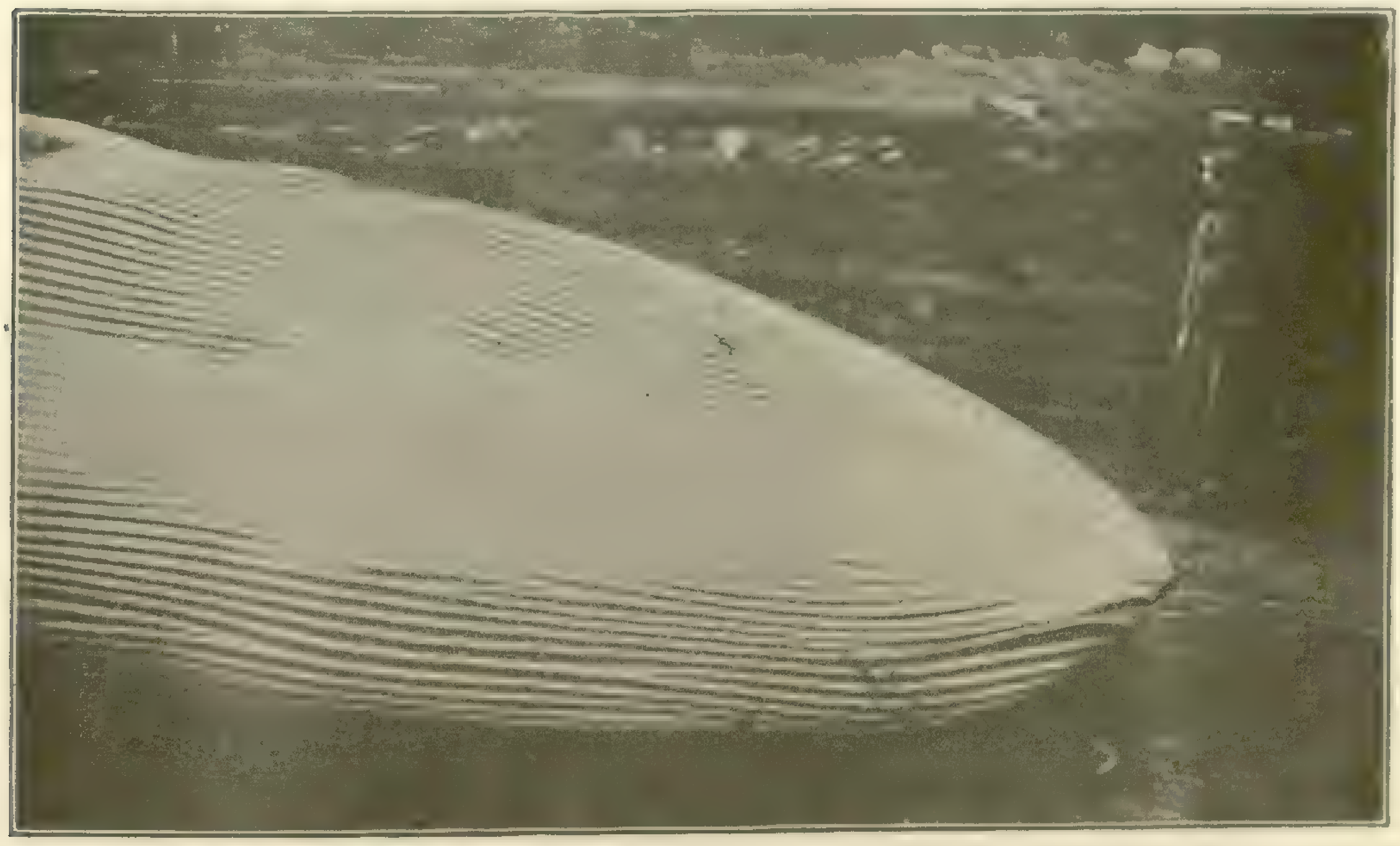

Fig. 6.— Throat of a finback whale.

therefore probably not far from the truth. The ordinary rate of swimming, however, is apparently a little less than this.

During my short stay at the Rose-au-Rue station six whales were taken and all were males. The men told me that at that season (September) the females seek the shallow and more quiet waters of the bays to bring forth their young, and their shyness at this time renders it difficult to approach them. Shortly before my arrival, at about September 4th, a female Finback whale (*Balænoptera physalus*) was killed which contained two calves nearly ready to be brought forth. They were said to have been male and female, about twelve feet long, and were

lying side by side in the uterus with the head of one by the tail of the other. This was the first time that a whale containing more than a single fœtus had been taken by the Company's steamers.

In addition to the photographs of spouting whales it seems worth while to introduce one showing the throat folds. These are usually represented in drawings as simple longitudinal plicæ. Figure 6 represents the ventral side of the throat in a Finback whale (*Balænoptera physalus*). The folds are seen to start from the border of the lips as single plications, but as the expanse of the throat increases posteriorly they fork dichotomously in a fairly definite manner, so that the number of folds at a given part of the center of the throat is greater than that at either end of the corrugated area. Posteriorly the folds run together in reverse order, so that a reduction is effected similar to that found at the anterior region of the throat. Curiously, however, forking may take place in either direction, so that the two new branches may point either anteriorly or posteriorly, but the latter mode of branching was not noticed in the posterior part of the area covered by the folds. Sometimes, also, two folds running parallel to each other may be connected by a short cross-fold, which aids in binding all together.

Up to the time of my visit the whaling steamer *Puma*, operating at Chaleur Bay and at Placentia Bay, had taken in 1903 107 Sulphur-bottoms, 66 Finbacks, 14 Humpbacks, and 1 Pollack whale (*B. borealis*). The last named was captured in Placentia Bay, as were the four taken in 1902.

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PHYSICAL IMITATIONS OF THE ACTIVITIES OF AMŒBA.

H. S. JENNINGS.

PHYSICAL imitations of the activities of lower organisms, such as are given us by Bütschli and Rhumbler, have always taken a place among the "startling achievements" of science. They arouse a lively interest in the popular mind as well as in the minds of men who are seriously studying the problems which such activities present. Anything which promises a bridge from the inorganic to the organic, from the physical to the vital, demands attention. Almost all men have definite convictions as to the relation of these two fields, — convictions which are foundational for the whole superstructure of intellectual or religious life; anything which touches these convictions must awaken interest.

How far have the physical imitations of vital activities gone? What do they really show as to relation of physical and vital? In the present paper such physical imitations as relate to one of the lowest organisms, Amœba, will be examined with these questions in view. The greater number of the physical experiments relate directly to Amœba, attempting to imitate its behavior. The writer has recently made a thorough re-examination of the behavior of this animal, the results of which have been published elsewhere (Jennings, :04), so that opportunity is presented for a comparison between the imitations and the reality. By determining to what extent the physical imitations throw light on the behavior of Amœba, we shall perhaps have a fair measure of what has been accomplished in this way, and of the promise for the future.

What is the real purpose of the physical imitations of vital activities? Clearly, the final purpose is to show what physical factors are at work in these activities. But this end may be followed in many ways; what is the special purpose of the imitations?

In the best cases the physical imitations arise as follows: There is first a study of certain vital activities. This is followed by construction of a hypothesis as to the nature of the factors at work, — an explanation of the activities in terms of phenomena already known. The third step is to determine by experiment whether the supposed known factors can produce such activities; these factors are combined in appropriate ways and the results observed. If they bring about activities similar to those shown in the vital phenomena, then the explanation gains much in probability, and we have an "imitation" of the vital activities. What the imitation shows is then, as Rhumbler ('98, p. 108) has well said, that the factors assumed to be at work really can produce such activities as we attribute to them, — and this is a long step in advance. There still remains the question whether the factors in our imitation actually *are* those at work in the vital phenomena.

To enable us to judge intelligently on this final question we need an accurate knowledge of the phenomena to be explained and of the forces at work in the imitation, that they may be closely compared; imitations founded on external resemblance are likely to be misleading. We have indeed three factors to be compared, — the explanation as it exists in the mind of the investigator, the physical experiment, and the vital activity. In the best cases these three must agree; the explanation fits the experiment, and the experiment is essentially similar to the vital phenomenon, so that the explanation fits the latter also. But the explanation given may fit the physical experiment and not the vital activity, or it may not even fit the experiment; we shall find examples of both these cases.

In the commoner case, where the explanation given does fit the physical experiment, how are we to judge whether the vital activity is to be similarly explained? Evidently an explanation based on an imitation can at best fit the vital activity only in so far as the latter agrees with the imitation. Points in which it does not agree must be attributed to other factors, and if these points are essential ones for the explanation given, then we must conclude that the vital activity is not explicable in the way proposed. Further, we must determine whether certain conditions,

preceding or following, which the explanation requires are actually fulfilled in the vital phenomena.

Imitations of the movements and of the variations in form have been oftenest attempted. Almost without exception the imitations are based on the hypothesis that these phenomena in Amœba are due to local changes in the surface tension of a fluid mass. Among the earliest experiments of this sort were those of Gad ('78). Gad placed drops of rancid oils (oils containing fatty acids) in weak solutions of alkali; for example, cod liver oil in 0.2 to 0.5 % sodium carbonate. As a result of the reaction between the fatty acid and the alkali soap is produced. This lowers the surface tension of the drop of oil here and there; as a result the drop changes form, sending out projections having an external resemblance to the pseudopodia of Amœba. A number of figures showing the forms taken by oil drops under these conditions are given in *Verworn's General Physiology*. Gad pointed out the resemblance of these forms to those shown by Amœba, but did not carry the matter farther.

Quincke ('79, '88) pursued further the study of movements caused in the manner just described, and put forth distinctly the view that the movements of Amœba (as well as of other protoplasmic masses) are due to similar causes. Quincke found that egg albumen might take the place of the sodium carbonate in the experiments above described; soap is then formed and movements occur as when the alkali is used. He held that Amœba is covered externally by a thin lamella of oil; that albuminous soaps are formed on the inner surface of this, thus decreasing the surface tension, and that the movements and changes of form are due to these changes in surface tension.

Most celebrated of all imitations of amœboid movements are those of Bütschli ('90, '92). Bütschli mixed slightly damp, powdered potassium carbonate with old olive oil, of a certain degree of rancidity, and brought drops of the mixture into water on a slide. (Directions in Bütschli, '90.) After standing twenty-four hours the drops are washed and new water or glycerine supplied. The drops now show streaming movements, send forth projections (see Fig. 1, *b*), and move about. The external resemblance to the phenomena shown in Amœba is

very striking. The movements are caused as follows: The potassium carbonate is dissolved by the water and acts on the oil, forming soap. Thus after a time the oil drop is permeated throughout by minute globules of soapy water, forming a foam-like emulsion. At times one of these globules of soap bursts on the outside of the drop of oil; the soap then spreads over the surface of the oil, lowering its surface tension in the region affected. At once a projection is formed here, currents flow from within the drop toward the region of lowered tension, and the entire drop may move in that direction.

Bütschli held that the movements of Amœba take place in a similar manner. He considers that protoplasm has an emulsion structure similar in a general way to that of the oil drops, — though of course the constituents are not the same. At times the meshwork enclosing the globules breaks at the outer surface of the Amœba, allowing some of the enclosed fluid to spread over the surface. This lowers the surface tension, causing Amœba to move in the same manner as the drop of oil.

Bütschli is inclined to attach much significance to the fact that the oil drops which move in the way described have a foam-like emulsion structure, and to consider this as a support to his view that the similarly moving protoplasm is similarly constituted. But such movements are by no means specially characteristic of fluids having a foam-like or emulsion structure; many drops having this structure do not show the movements, while other drops which have not this structure show the movements equally well, as we shall see. The movements require only that there shall be some method of producing local changes in surface tension; this may be easily brought about without the emulsion structure.

Bernstein (:00) produced similar movements in drops of mercury. Sufficient mercury to make a drop or disk five to ten millimetres in diameter is placed in a flat-bottomed watch-glass. Over it is poured some 20% nitric acid, and thereto is added a quantity of a strong solution of potassium bichromate. The mixture acts chemically on the mercury, lowering its surface tension. The intensity of the action varies locally, so that the surface tension is decreased now here, now there. As a result

the mercury moves and changes form in a striking manner, sending out projections or becoming wholly irregular, at the same time moving from place to place.[1]

The present author (:02) has given another method of observing such movements. A mixture of three parts glycerine and one part 95 % alcohol is placed on a slide and covered with a large cover-glass, supported near its ends by glass rods. Beneath the cover-glass a drop of clove oil is introduced by means of a medicine dropper drawn to a fine point. The alcohol acts locally on the surface of the clove oil, decreasing its surface tension here and there. As a result the clove oil drop changes form, sends out projections and moves from place in a striking manner. The phenomena shown are similar to those in Bütschli's drops of oil emulsion. The experiments are much easier to perform than those of Bütschli; by varying slightly the amount of alcohol in the mixture one can always be certain of getting marked results. But the movements do not continue so long as in Bütschli's experiments.

In all these experiments the movements are due to local changes in surface tension. When such a local change is produced on the surface of a fluid drop a characteristic set of currents results. From the region of least tension surface cur-

[1] The attempts of Herrera to imitate protoplasmic movements read almost like a travesty of those of the authors above mentioned. Herrera made a "synthetic protoplasm" by mixing together certain chemicals which analysis showed to exist in the protoplasm of one of the myxomycetes. This mixture contained "pepsine, ... peptone, acetic fibrine, oleic acid, soap, sugar, extract of bile, a considerable quantity of carbonate of soda, carbonates of calcium and ammonium, lactate of calcium, phosphates of calcium and magnesium, sulphates of calcium and iron, chloride of sodium, soap" (Herrera, '98, p. 118). When this miscellaneous conglomeration of chemicals was wet with water it showed, as one may well conceive, many diffusion currents. Herrera considers these as a "faithful reproduction of the internal movements of protoplasm described by Van Tieghem." In a later contribution Herrera ('98a) gives an imitation of amœboid motion based on the theory that Amœba is moved by the bubbles of carbon dioxide which it gives off in its respiration. Mix bicarbonate of soda with printer's ink so that a product is obtained having a sirupy consistency. Place on a surface wet with a weak solution of tartaric acid. Bubbles of carbon dioxide are produced, of course causing the mass to change form and move; "the illusion of a living being is complete." It is only just to say that Herrera later gave up the idea that the movements of Amœba are caused in this manner.

rents pass in all directions, while an interior current passes toward the region of least tension. The reason for these currents may be seen by imagining that the drop is covered with a stretched India rubber membrane in place of the surface film. If this stretched membrane is weakened or cut at a certain point the remainder of the membrane will pull away from this point, simulating the surface current. At the same time fluid from within will be pressed out at the weakened point, — thus simulating the central current toward the point of least tension.

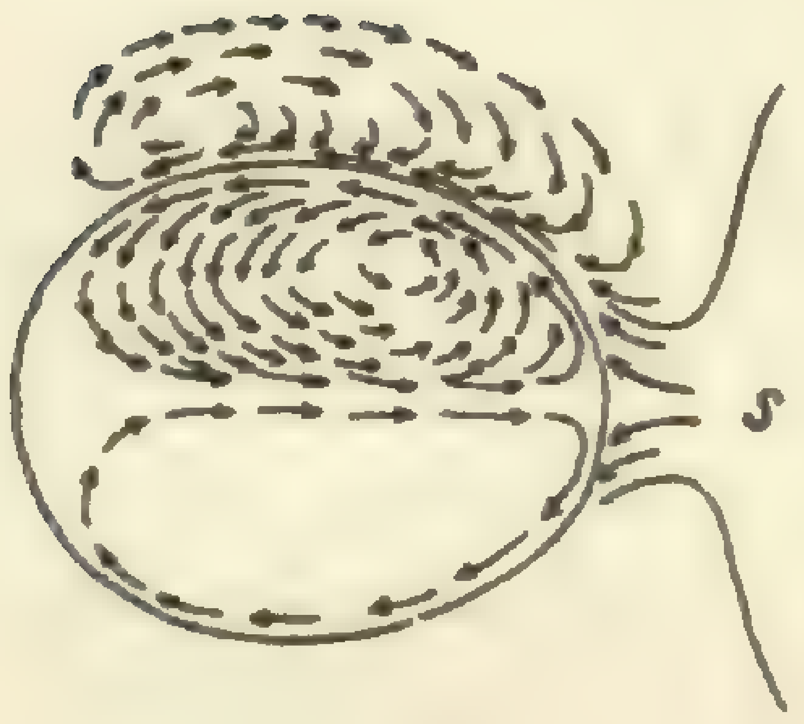

Fig. 1 *a.*

Fig. 1 *b.*

Fig. 1.— Currents produced by local decrease of surface tension, after Bütschli. *a*, Currents in an oil drop when the surface tension is decreased at one end by contact with a soap solution (*s*); surface currents away from the point of lowered tension; a central current toward this point. *b*, One of the drops of oil emulsion, showing the irregular form and the characteristic currents at the tip of each projection.

The characteristic currents may be seen in Bütschli's experiments or in those with the drops of clove oil, if some soot or India ink has been mixed with the oil. Such currents are represented in Fig. 1, taken from Bütschli. If the axial current carries forward more fluid than the superficial currents carry backward, the drop may elongate in the direction of the axial current and move as a whole in the same direction. This often occurs.

Such currents as are shown in Figure 1 are an invariable feature of movements of fluids due to local decrease in surface tension. Indeed, these currents are the characteristic phenomena; they may be the only movements that occur.

If, then, the movements of Amœba are really produced as they are in the imitations, by means of local changes in surface tension, we must expect to find in Amœba these characteristic currents. In an Amœba moving in a certain direction there should be a central current forward and superficial currents backward. In an extending pseudopodium the central current should be toward the point, the superficial currents away from it. Do such currents exist?

There is evidently a central current forward. But are the superficial currents backward, as the theory requires? In studying the movements from above, without the aid of experiment, it is difficult to determine this point. But there are certain appearances on the lower surface and at the lateral margins which give the impression that such backward currents may exist. In fact Bütschli, Rhumbler and others became convinced of the existence of such currents. The movements of Amœba were thus brought into full agreement with those of the drops moving as a result of local decrease in surface tension. This is brought out clearly by an examination of the figures of the currents in Amœba given by Bütschli and Rhumbler, copied in Figure 2. It was then almost inevitable to conclude that the same causes are at work in the two cases; that the movements of Amœba are due to local changes in surface tension.

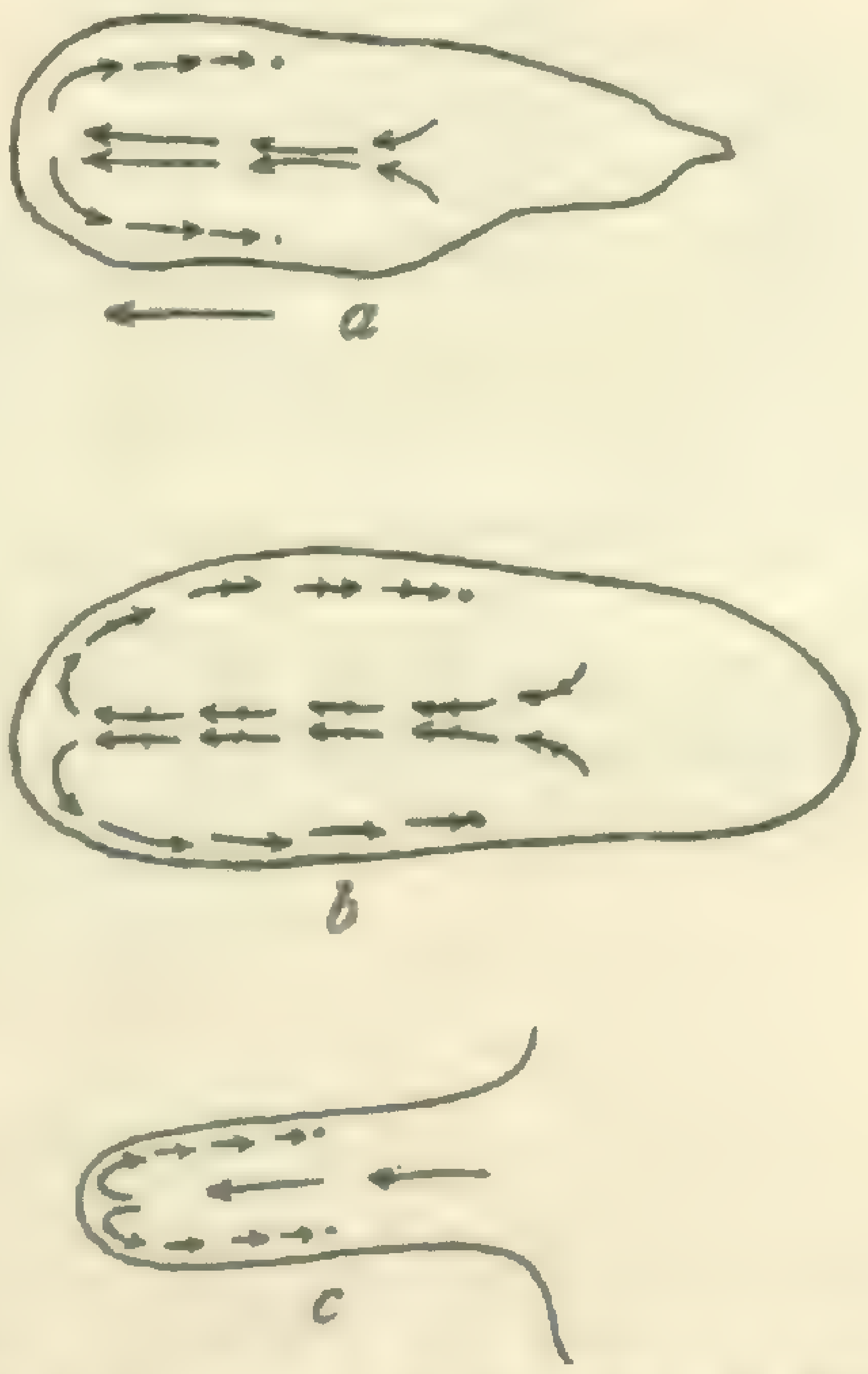

Fig. 2.— Diagram of currents in a moving Amœba, according to Bütschli and Rhumbler. *a*, Diagram of the currents as seen from above, after Rhumbler; *b*, diagram of the currents in side view, after Rhumbler; *c*, diagram of the currents in an advancing pseudopodium, after Bütschli.

In the extended experimental study of the activities of Amœba recently made by the present writer (:04), it was shown that the supposed backward currents of the surface do not exist. On the contrary, all parts of the surface which are not attached to the substratum are typically moving forward, in

the same direction as the central current, while the attached parts of the surface are at rest. The movement of Amœba is thus of a rolling character; the upper surface continually passes around the anterior end to form the lower surface; this then remains quiet until it is taken up by the posterior end as the latter moves forward. The movements in an advancing Amœba are indicated in Figure 3. In a projecting pseudopodium the movements are of the same character as those at the anterior end (Fig. 3), save when the pseudopodium projects freely into

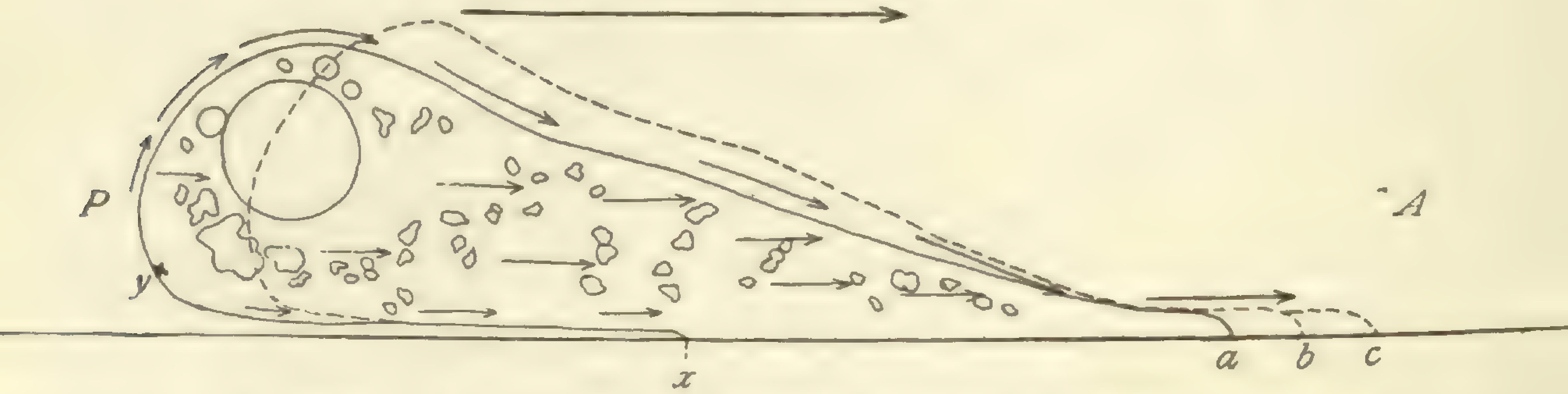

FIG. 3.—Diagram of the movements of an Amœba in locomotion, side view. The arrows show the direction of the currents; the longer arrows indicating more rapid movement. The large arrow above shows the direction of locomotion. The anterior end (A) is thin and attached to the substratum as far back as *x*; the lower surface from *a* to *x* is at rest. The posterior end (*P*) is high and rounded, and free from the substratum. *a*, *b*, *c*, successive positions occupied by the anterior end. The broken outline shows the position occupied by the Amœba a little later.

the water, being nowhere in contact with a solid. In the latter case the entire surface moves outward, in the same direction as the tip.

Details of the observations and experiments which demonstrate the movements to be of the character just set forth are given in an extensive paper published elsewhere (Jennings, :04). The movements were determined chiefly by observing the motion of objects attached to the outer surface of Amœba, of objects partly imbedded in the outer layer, and of particles within the body. The movements as thus studied are clear, and exclude the possibility of the typical existence of backward currents on the surface.

It appears then that Amœba does not move in the same manner as do the imitations based on local changes in the surface tension of a fluid mass. The currents which form the characteristic features in the latter case are not present in Amœba.

Neither theoretically nor practically does there appear to be any evidence that movements due to changes in surface tension can take place without these characteristic currents. We cannot then consider the movements of Amœba to be due to a decrease in surface tension at the anterior end, as in the "imitations." In precisely the feature which led to the supposition that the movements in the two cases were of the same character we find that there is actually an absolute contrast. In Amœba the surface currents are in the direction of movement of the mass, and in the same direction as the central current; in the imitations they are in the opposite direction.

Clearly the surface tension theory will not account for the phenomena as they actually exist. This becomes still more evident when we consider the formation of pseudopodia not in contact. In these there is not only no backward current, but also no resting surface; axis and surface move outward in the same direction as the tip. Such movements are not producible by local changes in surface tension. The "imitations" are imitations only to the extent that they are fluids and that they move; they are not imitations so far as the nature of the movements and their cause is concerned.

A much more nearly accurate imitation of the movements of Amœba may be produced with gravity as the active agent in place of surface tension. A drop of water moving down hill on a surface to which it does not cling strongly shows the same rolling movement that we find in Amœba. The lower surface (in contact with the substratum) is at rest, while the upper surface moves forward and passes continually around the anterior end to the lower surface. But we know that gravity is not the active agent in the movement of Amœba.

An imitation of the usual locomotion of Amœba that is accurate even to minute details is described by the present author in the paper on the behavior of Amœba already cited (Jennings :04). A drop of fluid resting on a substratum is caused to adhere to the substratum more strongly at one edge than at the other. Thereupon the drop moves toward the more adherent edge, and in so doing it shows exactly the form and movements of an Amœba in locomotion. The experiments may best be

performed as follows: A piece of smooth cardboard, such as the Bristol board used for drawing, is placed in the bottom of a flat dish and on a certain spot on the cardboard is placed a drop of water. The whole is then covered with bone oil. This soaks into the cardboard, except where the latter is protected by the drop of water. After the board is well soaked in oil the drop of water is removed, leaving the whole surface covered with oil some millimeters deep. Now a drop of water or glycerine, to which has been added some fine soot, is placed on the cardboard under the oil. This drop is allowed to come in contact by one edge with the area which had been protected from the oil. To this area it adheres, the edge in contact spreads out as a thin sheet, and the rest of the drop is pulled over to the area. Its movement is then exactly that typical for a flowing Amœba, so that Figure 3 would do equally well for a diagram of the movements of such a drop as for those of Amœba. The resemblance extends to minute details; many of these are set forth in the author's paper above cited (:04). Among other things, the formation of pseudopodia in contact with the substratum may be imitated by making the area to which the drop adheres at one edge very small; then a projection is formed merely of the width of this area.

But this imitation, like the others, fails when we take into consideration the formation of pseudopodia which are nowhere in contact with a solid. Projections corresponding to these cannot be formed in the physical experiments just described, for in these adherence to a solid is the essential point. Since the entire anterior end of the Amœba can be pushed out into the free water, we find that Amœba can perform all the active operations concerned in locomotion without adherence to a solid. This effectually blocks any attempt to explain the movements of Amœba as due, like those of the drops in the experiments just described, to one-sided adherence to the substratum.

Thus none of the physical imitations gives us a clue to the physical agent actually at work in the movements of Amœba. The experiments last described are perhaps useful in giving us an idea of the direction of action of the forces at work in producing locomotion. Not even so much as this can be said of

the surface tension experiments; the direction of action of the forces in these is evidently different from that in Amœba.

We may then turn to imitations of other activities of Amœba. Many attempts have been made to imitate certain of the reactions to stimuli — particularly the positive reaction to chemicals. Such imitations depend on the fact that a local decrease in the surface tension of a drop of fluid may be caused by contact with a chemical; the drop then moves in the direction of lowered tension. Some of the experiments based on this are the following:

Rhumbler ('99, p. 585) placed a small drop (60 to 90 μ in diameter) of castor oil in alcohol, and brought close to it the open end of a capillary tube containing clove oil, chloroform, or 5 % potassium hydroxide. The substance within the tube diffused out against the drop of castor oil and decreased its surface tension in the region of contact. Thereupon the usual currents were produced (Fig. 1), and the drop moved in the direction of lowered tension, finally entering the tube.

Bernstein (:00) placed a drop of mercury in twenty per cent. nitric acid, then brought near it a crystal of potassium bichromate. By the chemical action the surface tension on the side of the drop next to the crystal is decreased. Thereupon the drop moves rapidly over to the crystal, and may push it about from place to place.

In the drops of clove oil in a mixture of glycerine and alcohol, described above (p. 8), similar movements may be caused (Jennings :02). With a capillary pipette a little alcohol is brought near one side of the drop. This decreases the surface tension of the part affected; thereupon a projection is sent out toward the alcohol, and the drop as a whole moves toward it. If the drop is heated at one edge, by touching the cover glass near it with a hot wire, the clove oil moves toward the heated side, and may be induced to follow the wire for some distance.

In all these experiments the movement is due to local alterations in surface tension; the drop moves toward the region of lowest tension; there is a central current in the direction of locomotion, and surface currents in the opposite direction. In Amœba, on the other hand, as we have seen, the movements

cannot be considered due to local decrease in surface tension. There are no superficial currents away from the region toward which the animal moves, but all parts that are in motion move toward the object causing the reaction. (For details, see Jennings, :04.) The experiments do not imitate the essential features of the action of Amœba, and do not show us the causes at work in its behavior. The reactions of Amœba are not simple direct results of the physical action of the agents producing them, but are indirect, like those of higher animals.

Many imitations have been devised for the taking of food by Amœba. Rhumbler ('98) holds that the ingestion of food by Amœba is due to physical adhesion between the liquid protoplasm and the solid food. He shows that drops of all sorts of fluids take in certain solids in this manner. A drop of water placed at the edge of a plate of glass draws to itself and envelopes splinters of wood and various other solids which come in contact with it. Glycerine, oils, white of egg, gum arabic, mastax varnish, etc., are shown to do the same. A convenient way of showing this is to fill a capillary glass tube with the fluid, then to bring a small piece of the solid in contact with the free surface of the liquid at the end of the tube. The pulling of the solid into the liquid is due to the adhesion of the two, in connection with the surface tension of the liquid.

These experiments of Rhumbler show that food might be taken in this manner, not that it is so taken. Careful study shows that there is in most species of Amœba no adhesion between the protoplasm and the food body. Food is taken by actively enclosing it along with a small quantity of water; the fact that no adhesion exists between it and the protoplasm is strikingly evident, and occasions much difficulty in the ingestion of food. (For details, see Jennings, :04, and compare the similar account of food-taking by Le Dantec, '94.) Thus the experiments do not really imitate the essential features of the behavior in Amœba. Only in Amœba verrucosa and its close relatives is there evidence of adhesion between the animal and its food. But even here there is adhesion equally to bodies which do not serve as food and are not ingested, so that for the ingestion itself an additional factor is necessary.

One of Rhumbler's most striking experiments is an imitation of the method by which Amœba takes as food a long filament of Oscillaria, coiling it up and enclosing it. The Amœba settles down somewhere along the filament, lengthens out upon it, and bends it over, forming a loop. This process is repeated until the long filament forms a close coil within the Amœba (figures in Rhumbler, 1898, p. 211, Lang, :01, p. 39; a similar account with figure in Leidy, '79, p. 86). Rhumbler considers this remarkable process to be brought about as follows: The Amœba adheres to the filament. It lengthens out along it, just as a drop of water lengthens out along a filament to which it adheres. Owing to the surface tension of the fluid protoplasm, impelling it to take the spherical form, it pulls on the two halves of the filament, producing a thrust inward from both directions. Gradually the enclosed parts of the filament are softened in the digestive processes of the Amœba. The softened portion then yields to the thrust from both directions and bends, so that more of the filament can be pulled into the Amœba by the tension of its surface film. The Amœba then lengthens out farther, owing to adhesion; more of the filament is softened and yields farther, so that more is pulled in by surface tension. This process continues until the filament is completely coiled up and enclosed.

On the basis of this explanation Rhumbler devised an imitation of the process. A chloroform drop is placed in the bottom of a watch-glass of water. A long fine thread of shellac, obtained by heating two pieces of shellac in contact over a flame and rapidly pulling them apart, is brought in contact with the drop. The latter envelopes the filament in some portion of its length, then proceeds to coil it up, as Amœba does with the Oscillaria filament; after a time the shellac thread is completely enclosed within the chloroform drop. The mechanism of the process is conceived to be the same as that above given for Amœba and the Alga filament.

This experiment is an interesting example of one of the numerous difficulties which beset the worker along such lines, — of the fact, namely, that even the imitation may not agree with the explanation given. The coiling up of the shellac

thread by the chloroform is not explicable in the manner supposed by Rhumbler; the surface tension of the drop has really nothing to do with it. This is shown by the fact that such a thread of shellac is coiled up in exactly the same manner if submerged in a large vessel of chloroform, so that it is nowhere in contact with the surface film. The coiling up is apparently due to strains within the shellac filament, produced when it was pulled out, and to the adhesiveness of its surface when wet with chloroform. There are no corresponding factors in the Oscillaria thread; this will indeed, as Rhumbler has shown, straighten out again when released by the Amœba. The process by which Amœba coils up the Oscillaria filament must thus be of an essentially different character from that occurring in the experiment. The explanation given by Rhumbler may of course still be correct for the process in Amœba, though it is not correct for his imitation of the process.

Amœba does not ingest every small object with which it comes in contact, but exercises an evident choice as to the substances which it takes as food. Physical explanations and imitations of such choice have been given. We may notice especially those set forth by the present author (:02) in extension of certain experiments of Rhumbler. A drop of chloroform is placed in the bottom of a watch-glass of water, and with fine tweezers pieces of various substances are brought in contact with its surface. Some are at once taken in; others are not, or are thrown out if forced into the drop. Glass, sand, dirt, wood, gum Arabic, and chlorate of potash are rejected; shellac, paraffin, styrax, and hard Canada balsam are accepted. The selection or rejection depends upon the relative amount of adhesion between the solid object on the one hand and the chloroform and water on the other. Those which adhere more strongly to the chloroform than to the water are taken in; others are rejected.

These experiments show how choice might occur in an organism; they do not show how it actually occurs in Amœba. Food-taking is usually, as we have seen, not accompanied by adhesion between Amœba and the food, so that choice of food cannot be explained as due to the fact that some substances adhere while others do not.

Rhumbler ('98) has given a physical imitation of the taking in of a food body and of later giving off the undigested residue (defecation). A rod of glass covered with a thin layer of shellac is taken in by a drop of chloroform (as a result of adhesion). The shellac is dissolved off by the chloroform and the glass rod is then thrown out, since the chloroform does not adhere to it. This imitation, like the others, loses much of its force in view of the fact that food-taking is not usually due to adhesion and that substances which do not adhere are taken as food; defecation cannot then be explained as due simply to lack of adhesion.

In all the imitations thus far we find that the physical factors at work cannot be considered the same as those that are acting in Amœba. The imitations are such only in purely external features. There exist certain imitations, however, in which this has not been proved to be the case. Thus, Rhumbler ('98) found that when chloroform drops are placed in water, the water gradually passes into the chloroform, collecting in minute globules, which later gather in a larger drop. This larger drop is finally given off to the outside. This process Rhumbler considers analogous to the formation and discharge of the contractile vacuole in Amœba. The present author (:04) has described imitations of certain movements of the pseudopodia in Amœba, produced in liquids partly covered with a solid layer; these are hardly of sufficient general interest to be detailed here. The most striking experiments which can still be considered with some degree of probability to indicate the factors really at work in certain processes occurring in the Rhizopoda are undoubtedly Rhumbler's imitations of the production of Difflugia shells. Since these deal with an organism closely related to Amœba, they may be described here.

The experiments may be performed as follows: Chloroform is rubbed up with fragments of glass in a mortar until the glass is reduced to the finest dust. Then with a pipette drawn out to a small point drops of this mixture of chloroform and glass are injected into water. At once the grains of glass come to the surface of the drops so formed and arrange themselves in a single layer, without chinks or crevices, exactly as in the shell of Difflugia. The chloroform drop is thus covered with a shell

having a striking resemblance to that of Difflugia. In place of chloroform, linseed oil or other oils may be used. The drops must then be injected into 70% alcohol, since the oil would float on water.

The factors at work in the formation of the "artificial shells" are diffusion currents within the chloroform, the adhesion of the bits of glass to its surface, and the action of surface tension in arranging and fitting together the bits of glass. Studies of the process by which the shell of Difflugia is formed at the time of division of the animal seem to indicate that the same factors may be at work in the living organism. (See Rhumbler, '98, p. 289.)

Reviewing our results, we find that few of the experimental imitations of the activities of Amœba stand before a critical comparison with what actually takes place in the animal. Such comparison shows in almost every case that the factors at work in the imitations are essentially different from those acting in Amœba. In particular, almost all the imitations based on local changes in surface tension break down completely.

What are we to conclude from this fact as to the part played by surface tension in vital phenomena? The tendency has been of late to attribute more and more of a rôle among life processes to surface tension. Amœba has been the chief place where the important part played by surface tension seemed really demonstrable; the movements, the reactions to stimuli, the taking of food, and the choice of food, were all attributed to this and closely related factors. With the demonstration of the complete failure of surface tension to account for the phenomena that were chiefly relied on to prove its importance, the supposition that it plays an immensely important rôle in life processes loses much of its weight. Surface tension may of course, in a more refined way than was supposed for Amœba, still play the large rôle in vital phenomena that some attribute to it. In the meshes of Bütschli's protoplasmic meshwork, or in the muscle fibrillæ (Bernstein), it may perhaps do what is demanded of it. Possibly the study of surface tension is still the most promising field for detection of the physical factors underlying life processes. But the surface tension theory must come to us shorn

of the trophies of its prowess, — its supposed full explanation of most of the activities of Amœba, — and bearing instead the record of a complete defeat.

What positive results of value have the physical imitations of vital activities in Amœba to show? As we have seen, there are still two or three of these that may really give us a clue to the factors at work in the vital processes; at least this has not yet been disproved. Beyond this the positive results are of a very general character. The imitations show that a drop of fluid might, through physical factors, show locomotion, move toward certain agents and away from others, and exhibit choice in the taking in of certain substances and the rejection of others. But they do not show specifically through what physical factors the activities are as a matter of fact brought about in Amœba or any other particular organism.

The chief value of most of the attempted physical imitations is that of a trial. The method of trial and error is a method of progress in science as elsewhere. In these imitations a definite explanation of the phenomena is put on trial. The "trial" consists in a more careful study of the phenomena in question; it is as an inspiration to such study that the imitations are of great value. If as a result the explanation given is recognized as "error," that is in itself an advance; this particular trial will not need to be made again. Continued application of this method of trial and error must result finally either in the discovery of the real factors at work, or in the recognition that we are dealing with a new class of factors not found in physics.

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THE INFLUENCE OF THE MUTATIONS OF THE PLEISTOCENE LAKES UPON THE PRESENT DISTRIBUTION OF CICINDELA.

H. F. WICKHAM.

WITH the propagation of the late theories of life-zones founded upon temperature conditions, has come about a neglect of those considerations, of a more obscure though not less important nature, which we must recognize if we are to attain anything more than a superficial understanding of geographical distribution. The zonal theory as expounded by some of its more steadfast adherents has the apparent advantage of simplicity and moreover appeals directly to the 'practical man' since it is without doubt correctly assumed that most of our cultivated plants as well as numerous wild ones are limited to certain belts which are more or less closely coincident with the isotherms. The theory works well with agriculture in general, but it only imperfectly expresses the truth if we apply it to the natural distribution of Coleoptera on this continent. By natural, I mean original, in the sense of not being modified through the agency of civilized man; for cultivation and settlement have been potent factors in changing the range of numerous species, often resulting in the rapid extermination of the most characteristic types of a district and their replacement by others. Barriers which a few years ago were amply sufficient to prevent the intermingling of life of two nearby regions become no longer effective and the Faunæ and the Floræ become contaminated by the encroachment of strangers. Irrigation changes the nature of entire counties, lakes are drained, mountains are denuded of their forests and can no longer support the life which has been theirs for thousands of quiet years.

While it has been known for many years that the geological history of a given region has exercised a profound influence upon the present Fauna and Flora; while the effects of the Glacial

Epoch upon the life of this and other countries have long been recognized and carefully studied so that numerous distributional phenomena due thereto have thus been referred to their proper cause ; and although modern lines of insect migration are being mapped and their relative importance determined, there is nevertheless a vast amount of detail to be worked out in order that certain local problems may be understood. It is with one of these local problems that we have now to do.

Some years ago, as the result of several seasons' collecting in the Great Basin, I became convinced that the distribution of certain species of Coleoptera therein occurring could not be accounted for by the theory of zonal arrangement of life, but apparently had as ultimate cause some condition or combination of conditions which belonged to the geological rather than the present history of the area under discussion. With the aim of testing this belief, further collections were made and all available data bearing upon the matter were collated, in order that it might be seen whether or not the above conclusion rested upon tangible grounds.

The Great Basin is a vast area of interior drainage, lying between the Wasatch Mountains and the Sierra Nevadas. The climate is arid, the soil in general desert, the vegetation such as characterizes regions of like nature in other parts of the world, being marked by the preponderance of a few species of dry dwarfed shrubs and the absence of forests except on certain higher mountain ranges which ridge the basin here and there. Since none of the rivers rising within the basin empty into bodies of water outside the limits, one of the most common methods of introduction of extra-limital species — by migration along the line of a water-course — is eliminated, and the fauna is not exposed to this source of modification. The two great mountain chains which form the eastern and western rims have acted as barriers to free interchange of inhabitants with the districts lying beyond, though some have doubtless crossed the passes from time to time. The southern boundary is less abruptly limited, so that those species which are suited to desert tracts may readily enter from that quarter, while the northern rim is made up of the series of hills that mark the divide between the Great Basin and the Columbia River drainage system.

We have here, then, a great enclosed region which, though comparatively open to migrations from the north and south, is nearly closed against encroachment from the east and west except in those cases where man may be conceded to have been a factor. We should expect the more characteristic forms to show extensive north and south distribution or that they may be confined to the basin and the more accessible adjoining areas. Some species no doubt originated, as such, within the limits of the basin proper, and I believe that, in some cases at least, we can determine which these are. It is with certain forms of this nature — that is to say with true indigenes — that we have now to deal.

Two types of littoral beetles may be said to be very characteristic of the Great Basin and to be dependent upon the peculiar conditions that occur there in the way of saline and alkaline flats in connection with springs and lakes. These are the Cicindelæ of the *echo* type and the species or subspecies of Tanarthrus which belong with *T. salicola*. Neither of these genera is confined to the basin, Cicindela being of wide distribution and evidently of southern origin, while Tanarthrus is not known outside of the southwestern United States. Besides the forms of this latter genus described from the lake shores of the Great Basin, a few species of somewhat different aspect are known to occur in saline spots in California and Arizona. The species of Bembidium of the *henshawi* type have also, in my opinion, attained their present specific structures within the limits of the Great Basin and are not to be considered migrants from the outside. For the present, I prefer to leave out of the discussion all of those Coleoptera not directly connected with the existence of alkaline and saline lakes, since the problem of their dispersal or distribution is different, in some respects, from that concerning the littoral forms and needs a separate body.

I am prepared to go farther than the simple statement that we can correctly indicate certain species as having arisen, as such, within the limits of the Great Basin. I believe it is also possible to show that some of these have been inhabitants of the region for long periods of time, and that in the course of their existence they have been played upon by conditions which arose

as the consequence of geological changes; that we can point out the modifications which have taken place in the species and, to a considerable extent, we can trace the geological phenomena which are the fundamental or underlying causes of the modifications. Of course not all species will be equally affected by changes in their environment, nor will the modifications necessarily be parallel. Minute differences in the organic structures of insects indicate a probable diversity of physiological characters, and varying physiological activities may well modify such details as patterns of coloration or even the colors themselves.

As an example of an insect which has, in all probability, had its range determined and its specific characters modified by a series of geological changes, the history of which is not too remote and therefore fairly well known, we may take that aggregate of forms of Cicindela described under the names *C. echo* Casey and *C. pseudosenilis* W. Horn. These are without doubt modifications of one type; in fact they are so closely related as to be separable only in series. They are also very close to *C. willistoni*, and are ranked as races thereof by Dr. Walther Horn. However, the exact status of these names, specific or subspecific, does not concern us at present; the fact remains that these forms are closely related and may well have come from a common stock. *Cicindela fulgida*, to which *willistoni* was formerly referred as a variety or race, is readily separable by the thickly haired front. It may perhaps be an older offspring of the same stem.

The ways in which the beetles differ from one another may be briefly outlined, in order that the reader may understand the relationships and the better appreciate the account of the variations of each. It must be borne in mind that the descriptions refer more especially to series of specimens than to individuals, unless definitely stated to the contrary.

Cicindela fulgida Say. Easily separated from the allied species by the front being thickly hairy. The color is usually more coppery red, though specimens occur at Lincoln, Nebraska, in which the ground color is nearly black. Markings moderate, rather narrow as a rule, the middle band not expanded along the margin (or but very slightly so), the humeral lunule very oblique

behind. This species belongs especially to the broad strip of plains lying to the eastward of the Rocky Mountains. It is known from Wyoming, Colorado, Kansas, Nebraska and New Mexico, but has not been reported from Central America nor from Old Mexico.[1]

Cicindela willistoni Leconte. A little stouter than *C. fulgida*, the color much less metallic. The front is sparsely haired; these hairs are readily lost, but the group of large punctures from which they spring may always be made out with little difficulty. Markings broader, the humeral lunule and median band always united along the margin; the apical lunule, also, usually, but not always, connected on the outer edge with the expanded marginal portion of the middle band. The tip of the humeral lunule (in those specimens in which it is free) is much less oblique than in *C. fulgida*. This insect is known only from the beaches of small lakes near Medicine Bow, Wyoming, where it was taken first by Dr. Williston, next by Mr. Warren Knaus and lastly by myself. I am not certain which of the little lakes was visited by Dr. Williston. He gives the locality Como Lake, but the usage of the village is not uniform and it may have been any one of three small lakes which lie within about twenty miles of one another. Mr. Knaus and I visited the one near the old station of Aurora, now several miles from the track. He calls it Como Lake,[2] while I have followed the prevailing custom of the villagers in speaking of it as Aurora Lake.

Cicindela echo Casey. Form of body nearly that of *C. willistoni*. Color brownish with an obscure purplish or coppery overcast. Front very sparsely hairy, the hairs being so readily removed that most specimens show only the punctures whence they originate. Markings usually rather narrow, the humeral lunule not or but slightly oblique at tip, middle band attaining the margin, usually but slightly dilated thereon but occasionally reaching the humeral lunule though not quite attaining the apical one which is complete. My series from Great Salt Lake (the original locality), most of which I collected at Saltair, in

[1] It is not included in Dr. Walther Horn's List of the Cicindelidæ of Mexico, *Jour. N. Y. Ento. Soc.*, Vol. 11, p. 213.

[2] *Entomological News*, Vol. 13, p. 147.

June, shows quite a good deal of variation in the markings, the changes chiefly affecting the middle band. The marginal portion of this band is variously developed so that it may reach quite to the humeral lunule and almost to the apical one, or it may not be expanded at all. The discal part may be quite rectangularly or very obliquely bent near the middle and the terminal knob-like appendix may be abruptly formed and angularly bent from the stem or it may appear simply as an enlargement, without being noticeably deflected at all. A set from Humboldt Lake, Nevada, taken by myself in June, while not identical with the Saltair forms, shows a range of variations almost exactly corresponding thereto, all of the important features of the one being duplicated in the other.

On the shores of Honey Lake, near Amedee, California, I took a fine series of Cicindela which I refer, for convenience, to *C. echo*, though they are not typical. The form is nearly the same and the ground colors are about alike, but the Amedee specimens almost entirely lack metallic gloss and the surface sculpture of the elytra is notably shallower. The Amedee beetles also differ, as a species, from the Saltair specimens in the broader markings, the greater obliquity of the median band (the terminal knob less deflected), and in the expansion of this band along the margin so as to connect broadly with the humeral lunule. The apical lunule is free in all of my specimens. One individual is entirely blackish, except that each elytron bears two small spots, one of which represents the anterior portion of the humeral lunule, the other the posterior part of the apical.

Cicindela pseudosenilis Walther Horn. Green, shining, a few varying to brownish or reddish. Form of body as in *C. echo*. Front of head sparsely hairy. The elytral markings are very close to those of the Saltair *echo*; the middle band does not show a distinct tendency to spread along the margin in any of my specimens, so that it is not connected with nor closely approximated by the apical and humeral lunules. The chief variations are those exhibited in the descending portion of the middle band, for though this band is usually rectangularly bent the terminal knob shows numerous modifications. In some

specimens this knob is largely developed though not hooklike, in others it disappears entirely, so that the descending part of the band is of nearly uniform size to the tip. None of the specimens in my series show a strong tendency towards the *willistoni* type of marking, the lead to that form going through *C. echo.* But some of the *pseudosenilis* approximate the Saltair *C. echo* so closely that if they were mixed they could scarcely be separated again. The shores of Owens Lake, in southeastern California, are the only definitely known haunts of the true *C. pseudosenilis*, though Dr. Howard writes me that in the National Museum is a single specimen said to have been taken by Mr. Coquillet in Los Angeles County — not very far distant. None of the other Californian collectors have found it in this latter locality, however. I found it in great abundance about the overflow of a spring on the upper beaches of Owens Lake, but none occurred in the immediate vicinity of the bitter waters of the lake itself.

Now that the variations of the insects have been described, we must turn again to the geological records and see what can be said of the early conditions of the country they inhabit. The geology of the Great Basin has been worked out by Dr. G. K. Gilbert,[1] and Dr. Israel C. Russell,[2] the results of their labors appearing in two fine volumes from which the main geological items used in this discussion are compiled. We find that in the early Pleistocene the basin held two great freshwater lakes: Bonneville, covering the greater part of western Utah and a small portion of eastern Nevada and southern Idaho, and Lahontan, occupying an extensive area in western Nevada and eastern California. Between them lay a broad plateau or divide, forming a watershed, the hydrographic basins of the lakes being contiguous. Both of these lakes were of irregular shape, Lahontan being especially so, with numerous arms and bays extending up narrow, flooded valleys. Each lake had two great periods of high water, which had been preceded by times of drought and desiccation, the second stage of flood being higher than the first. These times of plenty correspond to the two

[1] *Lake Bonneville.* Monographs of the U. S. Geological Survey, I, 1890.

[2] *Geological History of Lake Lahontan.* Monographs of the U. S. Geological Survey, XI, 1885.

glacial epochs of the Sierra Nevadas, though the climate is supposed to have been only moderately humid and rather cold. The increase in the size of the lakes is not ascribed to the melting of the glaciers, though this must have added considerably to their volume, as the ice cap was not large enough to furnish so much water. While Lake Lahontan seems not to have overflowed, Lake Bonneville broke through the barrier to the north and found an outlet to the sea by way of the Columbia River basin.[1] The desiccation of the lakes during the dry times is thought to have been more complete than at present.

The relation of our modern lakes to those of Pleistocene times is principally that of occupying the same area; that is to say, the bodies of water now existent have, in the main, been formed since the old lakes dried up, and are not to be considered remnants left by incomplete evaporation, since in the latter case the waters must have been much salter than they are. An exception may perhaps be made of Great Salt Lake, the evidence being inconclusive; and I have no data of this nature concerning Owens Lake and Mono Lake, which never formed part of these two larger bodies, but were separate even during the high-water periods of the Pleistocene. The littoral Fauna may easily have been preserved, even through times of great drought, by clustering about the edges of springs. In this way, even to-day, we know that some are carried over; for example, this very *Cicindela echo* flocks on the damp ground in the vicinity of the little springs about the edge of the now dried-up Humboldt Lake. Many springs are of a far more permanent nature than the shallow lakes into which they discharge, and I think that we may safely assume that they lasted, in many instances, through the times of most complete desiccation.

Now let us consider the relation of existing lakes (which have been examined for material for this paper), and those of ancient times, in order to see what opportunity the beetles have had for differentiation through isolation. I have visited Great Salt Lake, Utah Lake, Humboldt Lake, Honey Lake, Walker Lake,

[1]This may possibly account for the present occurrence in the Columbia district of such widely distributed Great Basin species as *Cicindela hæmorrhagica* and *Saprinus estriatus*.

Owens Lake and Mono Lake, and found *Cicindela echo* or *C. pseudosenilis* at all but three — namely, Utah, Mono and Walker. I cannot definitely assert that the species, in some of its forms, is absent from all of these three, but we have no evidence to show that it occurs there. Mono Lake may perhaps lie at too great an altitude for the insect to flourish, or it may never have been introduced into the district. It is possible that a more extended search may yet disclose some form of it there, my visit having been a hurried one and productive of no Cicindela whatever, though *C. pseudosenilis* and *C. hæmorrhagica* must have been flying in abundance at Owens Lake, distant about a hundred miles. Walker Lake has been twice visited by me with the special object of looking for some form of *C. echo*, but I took only *C. hæmorrhagica* and a variety of *C. oregona*, both in plenty. I hope that if any entomologist has the opportunity, he will visit the flats at the upper end of the lake, in the vicinity of the mouth of the river, since I have noticed that the colonies are sometimes confined to a limited area and may easily be missed. It will be well also to examine the neighborhood of the large spring said to exist near Wabuska; it dates back to considerable antiquity and may yield something interesting. Utah Lake has been visited by several entomologists at different times, and it seems that if *C. echo* occurs there it should have been met with before this.

These three lakes which have failed to yield material after exploration may be left out of the rest of the discussion. Of those which have been productive, Owens Lake has been distinct for a vast period, having, as we have seen, been separate even during the greatest extension of the others. Great Salt Lake was a part of Bonneville, while Humboldt Lake and Honey Lake lie in the ancient bed of Lahontan. The small bodies of water in Wyoming, which harbor *C. willistoni* were of course not included in either and had no communication therewith.

Looking again at the beetles, we find:

(a) The Owens Lake form, which has probably been isolated since (at least) early Pleistocene times, is sufficiently well differentiated to have been separated by systematists as a distinct species, though this view is no longer held.

(b) The form from Honey Lake, on the extreme western border of the old Lake Lahontan, is also well differentiated, though not in the same way. This lake is extremely shallow and evanescent, having dried up at least twice within the memory of the present generation, and has no doubt been separated from the main body of the old lake since a comparatively early period in the second great decline in size of the latter. The beetles live about the seepage on the lake beach that comes from the hot springs a few hundred yards distant. While it is impossible at present to point out the details which lead to variation in any one direction, it is evident that local conditions, aided by long isolation, have so modified this form that it is now readily separable, in series, from those taken elsewhere.

(c) The specimens from Humboldt Lake, farther to the east, are more of the type of typical *echo*, differing but little from the series taken at Great Salt Lake, Utah, whence the species was originally described. While the Humboldt colony must have been separate from the latter for a great length of time, it has been comparatively little differentiated therefrom. The reason for this cannot now be assigned. It may be that the local conditions requisite to incite variation were not present, or perhaps the two colonies have simply varied along parallel lines. Though isolation is unquestionably favorable to differentiation, it does not follow that every isolated colony must differ from every other. It is well known that with certain species of Cicindela some colonies produce mostly specimens of one type, others will produce those of another, while a third will be composed of a mixture of both, with all the intergrades.

(d) The form from Great Salt Lake, to which the name *C. echo* is properly applied, is not like that from Owens Lake nor that from Honey Lake, though closely approached by the specimens from Humboldt Lake.

(e) On the shores of the small lakes in Wyoming, we have *C. willistoni*, a closely related form occurring (as far as we know) nowhere else, which according to geological evidence can scarcely have had any communication with the Great Basin colonies during Pleistocene times. I am inclined to look to a still more remote date for the cause of this phenomenon, and con-

sider *C. willistoni* a survivor of an early stock which, during the Tertiary period, inhabited the present Rocky Mountain region and in all probability the adjacent districts to the east and west at the time of the great extension of the Tertiary lakes. *C. willistoni* is much better differentiated from the races of *C. echo* than those races are among themselves.

My conclusions are these: That in *C. echo* (with its several races, including *C. pseudosenilis*) and *C. willistoni*, we have two branches of a stem which were probably separated by some of the orographic movements which gave rise to the upheaval of the Wasatch and Rocky Mountains. That this stem form was a littoral species and the branch remaining in the Great Basin was carried over the interval between the dissolution of the Tertiary lakes and the appearance of the great Pleistocene lakes by clinging to the borders of springs and other bodies of water. That with the growth of Lake Bonneville and Lake Lahontan and the contemporaneous filling by water of the smaller basins, it spread over the whole habitable area between the Wasatch and the Sierras. The subsequent desiccation of the greater part of the Lahontan and Bonneville basins left a series of smaller lakes of varying permanence and more or less complete isolation. Local conditions, acting on the members of colonies of the beetles thus separated from their neighbors, have given rise to variations of different kinds and certain of these variations have been preserved and accentuated through this isolation. As a consequence, we have the phenomenon of local races, strongly or slightly marked according to the strength of the conditions exciting variability and to the comparative degree of isolation of the colony after a certain character had made its appearance. Owens Lake and Honey Lake, having been long since separate from the larger bodies and presumably subjected to different conditions, climatic and otherwise, because of their proximity to the Sierras, have at length produced upon their shores racial types which are easily distinguished from each other and from the forms found farther east.

If the species of Cicindela used in illustration were alone in presenting the general phenomena noticed, one might well doubt the sufficiency of the evidence adduced in support of the foregoing

conclusions: and as the matter stands, I am well aware of the circumstantial nature of much of it and of the many possibilities of wrongly interpreting the facts. However, I have been collecting and studying other species of littoral Coleoptera in the Great Basin, with a view to further prosecution of the problem, and find much in corroboration. It is evident that the same general law is followed in the variations of Tanarthrus, and I hope also to demonstrate a parallelism in certain Carabidæ and Histeridæ which are associated with it.

STATE UNIVERSITY OF IOWA,
Iowa City, March 19, 1904.

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. E. L. MARK, DIRECTOR.— No. 154.

A SIMPLE APPARATUS FOR AËRATING LIQUID SOLUTIONS.

S. O. MAST.

In studying the effect of dilute and concentrated solutions of sea water on marine algæ it became necessary to aërate the solutions in order to keep them fresh. For this purpose a very simple piece of apparatus was devised. The apparatus was used slowly to concentrate or dilute the solutions as well as to aërate them. It has now been in continuous operation for over three months and has proved to be so effective, to require so little care, and to be so easily made, that a brief description of it may be useful to others.

The general structure of the apparatus will be readily understood by referring to the accompanying figures. It will only be necessary then to discuss a few details of its structure and the principles on which its operation depends.

The aërating tubes used in the experiments mentioned above are 90 cm. long and 4.5 mm. in diameter (inside measure), which is constricted to 0.5 mm. at a point 7 cm. from the upper end. The capillary siphon is 0.75 mm. in diameter; the solution in the culture jar is 27 cm. deep. It will readily be seen that, since the aërating tube is much larger than the capillary siphon, if both are to be constantly full the solution must flow much more slowly in the tube than in the siphon.

Owing to the action of gravitation, however, the motion of the solution tends to accelerate as it falls, and therefore tends to flow faster in the aërating tube than in the siphon; so that the solution in the tube as it flows through the constriction is broken into very short columns separated by small bubbles of

air, which incidentally aërates the solution. Several of these columns unite, forming larger ones as they flow down the tube, as do the bubbles also. The relative lengths of these

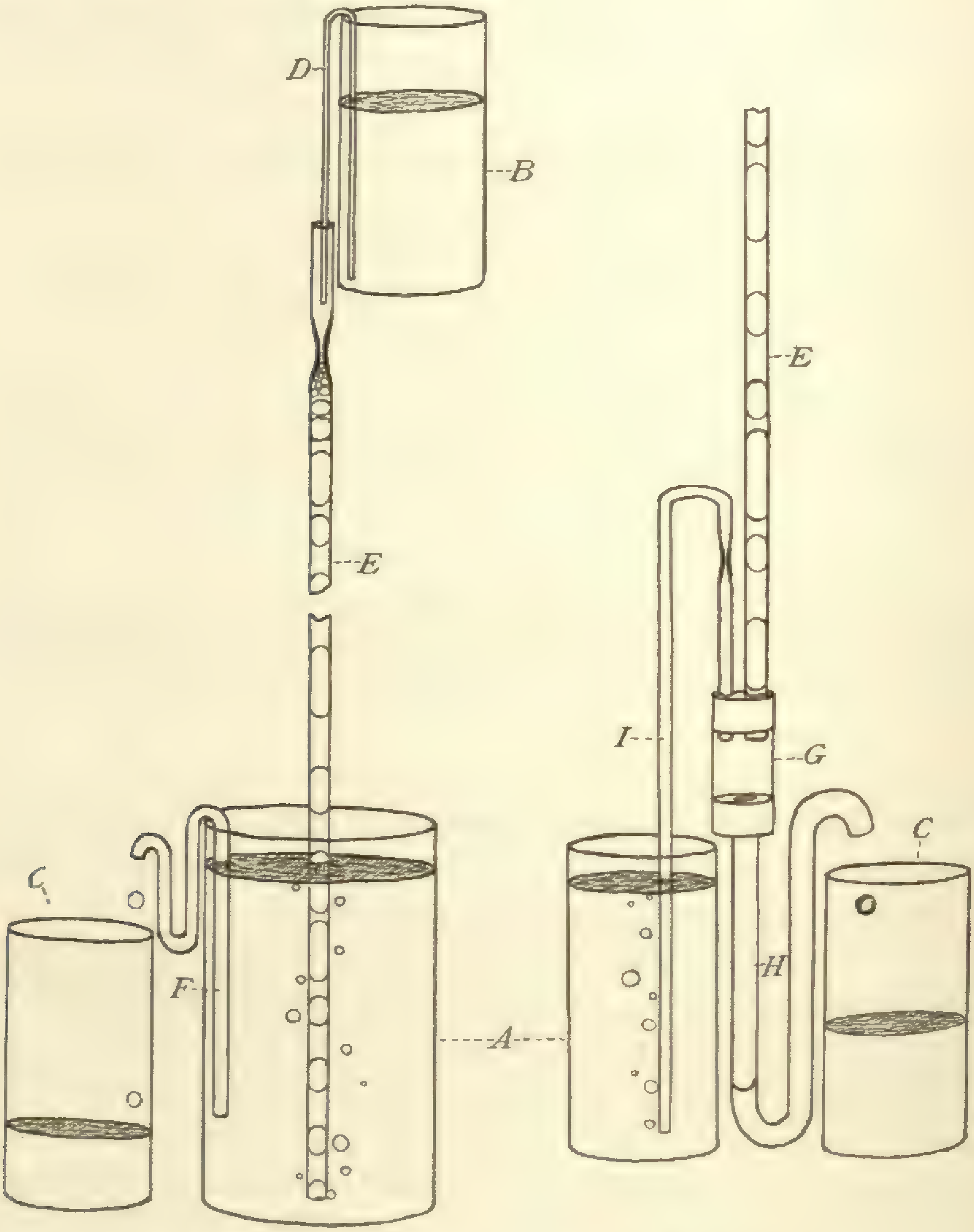

FIG. 1. FIG. 2.

FIG. 1. — An aërating apparatus in which the liquid used to aërate flows into the culture jar.
FIG. 2. — A similar apparatus in which the liquid does not flow into the culture jar. *A*, a culture jar, *i. e.*, a jar containing a solution to be aërated; *B*, a supply jar; *C*, an overflow jar; *D*, a capillary siphon; *E*, an aërating tube; *F*, a constant-level siphon; *G*, *H* and *I*, accessories to the aërating tube.

columns of solution and spaces of air depend upon three factors: (1) The difference between the diameter of the capil-

lary siphon and that of the aërating tube, (2) the length of the aërating tube, and (3) the depth of the solution in the culture jar. All that is necessary in order to increase the amount of air, as compared with that of the solution in the tube, is to increase either the diameter or length of the aërating tube or to decrease the depth of the solution in the culture jar.

If the diameter of the tube is increased and the flow kept constant it is clear that more air must be taken in to fill the increased space due to the enlargement. But as the diameter increases the adhesive force between the walls of the tube and the solution in it decreases, as compared with the cohesive force of the solution, so that when a certain diameter is reached the bubbles of air break through the columns of solution and thus can no longer be forced to the bottom of the tube in the culture jar. As a matter of fact, the maximum limit of diameter in the case of water is practically about 4.5 mm. Further, if the rate of flow in the aërating tube be in any way increased while that in the siphon remains constant, more air will be required to keep the tube full, just as in case of an increase in diameter. The rate of flow in the tube, however, varies directly with the length of the tube; and since there is no theoretical limit to the possible length of the tube, the amount of air compared with that of solution can be theoretically increased indefinitely. The depth of the culture solution is really a function of the length of the aërating tube. In order to overcome the pressure of the culture liquid and force the air out at the bottom of the aërating tube, it is necessary to have a column of solution in the tube *above* the level of the solution in the culture jar slightly greater than the air space in the tube *below* that level. Consequently the portion of the tube which is below the level of the solution in the culture jar and enough of it above that level to contain as much solution as there is air below, have nothing to do with increase in acceleration due to gravitation, for they simply balance each other, and therefore these parts are not effective in increasing the amount of air introduced. This being true, it will readily be seen that increasing the depth of the culture solution has the same effect as decreasing the length of the aërating tube, and that therefore the deeper this solution, other things being equal, the less will be the air forced through.

The purpose of the constriction in the aerating tube is merely to break up the column of solution in the tube. If this were not thus broken up it would accumulate until it became slightly greater than the air spaces in the tube below the level of the culture fluid and then would suddenly flow down, forcing the air out with a rush, after which it would again accumulate, flow down, etc. This is just what happens if the constriction is not small enough in comparison with the size of the capillary siphon. A few experimental trials, however, will be sufficient to enable one to decide on the proper relative sizes of the two. No definite instruction can be given with reference to this since the diameter of the siphon must vary with the diameter and length of the aërating tube and with the depth, specific gravity and viscosity of the culture solution. In general the constriction should be somewhat smaller than the siphon.

In some forms of apparatus[1] the lower end of the aërating tube is bent on itself so as to project upwards in the culture solution and a small piece of sponge is then pressed rather tightly into this bent free end, or the tube may be drawn out into a capillary ending. It is claimed that the sponge, especially, breaks up the air into very small bubbles. This is undoubtedly true, but it has been found that in the apparatus represented in Figures 1 and 2 the pressure required to force the air through the sponge is so great that the value of this adjunct is questionable.

The most efficient and simplest method discovered to break up the air bubbles is as follows: Cut off the lower end of the aërating tube square, grind it quite flat, and let it rest on a firm piece of rubber, leather, or wood on the surface of which a considerable number of radiating grooves has been made. The piece of rubber rests on the bottom of the culture jar and the tube is placed over the point whence the grooves radiate. The grooves in any event must be narrow. Their depth should depend upon the weight of the aërating tube. If the tube is heavy it will sink into the surface upon which it rests, and therefore under such conditions the grooves must be deeper than if the

[1] See H. Lenz. Verbesserung an den Durchlüftungsapparaten der Seewasser-Aquarien. *Zool. Anzeiger*, 1879, Jahrg. 2, pp. 20, 21.

tube is light. Although by this device the bubbles are not broken up as much as they can be by using a piece of sponge forced into the end of the tube, this method has the decided advantage of requiring much less pressure, and there is also much less danger of clogging the tube than if a sponge is used.

In making the aërating constriction the tube should be heated, without being drawn out, until the walls fall in, as this causes them to become much thicker and consequently stronger than they otherwise would be.

It is much better to use a capillary siphon than a larger tube drawn out to a capillary ending; first, because a capillary siphon never needs to be filled, for when the supply jar is filled to within about 1 *cm.* of the top capillary attraction will fill the siphon and start it running; secondly, because a large tube drawn out at one end is much more readily clogged than a small one of equal diameter throughout.

The constant-level siphon (*F*) should be unquestionably large enough to drain off the solution as fast as it comes into the culture jar, but not much larger; neither should its outer end be more than a few centimeters lower than its highest point, for if it is the decrease in pressure at the highest point causes sufficient increase in vapor pressure of dissolved gases to cause them to be thrown out of solution, to collect at this point, and thus to clog the siphon.

The principles of operation in the second apparatus, that, represented in Figure 2, are in all respects similar to those discussed with reference to the apparatus represented in Figure 1. The upper end of the aërating tube, the capillary siphon, and the supply jar are the same as represented in Figure 1.

The chamber *G*, which serves to separate the air from the liquid, can be readily made by cutting off a test tube. It should be about 1.5 cm. in diameter and 4 or 5 cm. long. It must of course be air-tight. Ordinary corks soaked in paraffin will serve very well to close the ends.

The tube *H* should be at least 5 mm. in diameter, slightly larger than the aërating tube proper, *i. e.*, large enough to prevent air being forced through it with the solution. Its length must be such that its outer end is somewhat farther above its

lower bend than the outer end of the tube *I* is below the surface of the solution in the culture jar; for if it is not the air will pass out through it instead of through the culture solution.

The tube *I* serves to convey the air from the chamber *G* into the culture solution. It may be of any size, length or form. The lumen through the constriction in it is very small; though not absolutely necessary, it serves to cause a more steady flow of air. A rubber tube with an adjustable pinch-cock might serve this purpose still better.

All that is necessary to operate either apparatus described, is to pour the solution from the overflow jar into the supply jar from time to time. The frequency required in this operation depends of course upon the size of the jars and the diameter of the capillary siphon. If, as in the experiment mentioned above, 4-liter jars and a 0.75 mm. siphon are used, a transfer once in three days will be quite sufficient.

In closing I wish to thank Dr. E. L. Mark for furnishing material which made the experiments referred to above possible, and for valuable criticism of the manuscript of this article.

SPIRE VARIATION IN *PYRAMIDULA ALTERNATA*.

FRANK COLLINS BAKER.

I. Introduction.

The object of the present investigation has been to ascertain by quantitative means the amount of variation in the same species of a pulmonate mollusk from several localities. For this purpose the shell of the common species, *Pyramidula alternata*, has been selected, as that species shows a large amount of variation in the form of the shell, particularly in the height of the spire.

Among the mollusks little biometric work was done previous to the year 1898. Since that time this group of animals has been receiving marked attention and several exhaustive papers have been published, notably those by C. C. Adams on Io and C. B. Davenport on Pecten. These papers, however, have dealt with marine or fresh water forms; in this investigation the biometric study has been applied to an air breathing land mollusk.

II. Material.

The material used in this investigation, *Pyramidula alternata* Say, was secured from the following localities:

1. Rochester, New York, on the steep hillside of the "Pinnacle" and the banks of the lower Genesee River. This locality is heavily wooded and there is a large accumulation of fallen logs and the ground is covered by a rich, black loam. Collected by the writer.

2. Auburn, New York, in damp, low, flat woodlands. Collected by Dr. Howard N. Lyon.

3. Bowmanville, near Chicago, Illinois, in flat woodlands. The timber is large and heavy, the ground is strewn with fallen

logs and the soil is a rich, black loam. Collected by the writer. The shells studied are not of uniform size, although they are nearly all adult measuring from twelve to twenty-four millimeters in diameter. The young shells of this species always have a flat or nearly flat spire, and as they would materially affect the results they were excluded.

In *Pyramidula alternata* we find a good example of variation caused by individual environment. The species lives for the most part under started bark, in crevices and under flat-lying tree trunks; hence its shell varies with its abode. For example, a specimen living between the "started" bark of a tree and the tree trunk, the space being very narrow, measured 23 × 11 mill., the height being about 48 per cent. of the width, while another specimen living under a fallen tree trunk measured 15 × 13 mill., the height being about 87 per cent. of the width, or 39 per cent. more than the first example. These specimens were from the same locality and from adjacent trees. Their habit of crowding into narrow crevices and between the bark and the tree trunk has caused this species to become one of the most variable of land shells as regards the form of the shell.[1]

On account of the extreme variability it was thought that a quantitative study of material from several rather widely separated localities would produce results of some interest. This species has a wide geographic range, being found throughout the eastern and central parts of the United States and Canada. Its western limit is said to be Minnesota.

III. Method of Obtaining Quantitative Data.

To obtain a variation index the diameter and altitude of the shell was measured in millimeters and the altitude divided by the diameter; *i. e.*, $\frac{\text{altitude.}}{\text{diameter}}$ The per cents. obtained in this way provide the shell index. In the diagrams the individuals or classes having the same per cent. are indicated on the horizontal line and the number of specimens in these classes (the frequencies) are indicated on the vertical line.

[1] See *Nautilus*, Vol. 10, p. 63, for a good article on this subject by C. C. Ormsbee on "Influence of Environment upon the Form and Color of Helix alternata."

The number of specimens available for this study has not been as large as is desirable in investigations of this kind; but as the three lots are of about the same number the results will not be materially affected.

In the tables of data the per cents. are indicated by a numerator and the individuals or frequencies having the same per cent. is noted as a denominator.

IV. Discussion of Data.

The Rochester Shells.

Figure 1.

The shells from Rochester show a rather wide range of variation, as is seen in Fig. 1, which is strongly trimodal. The most

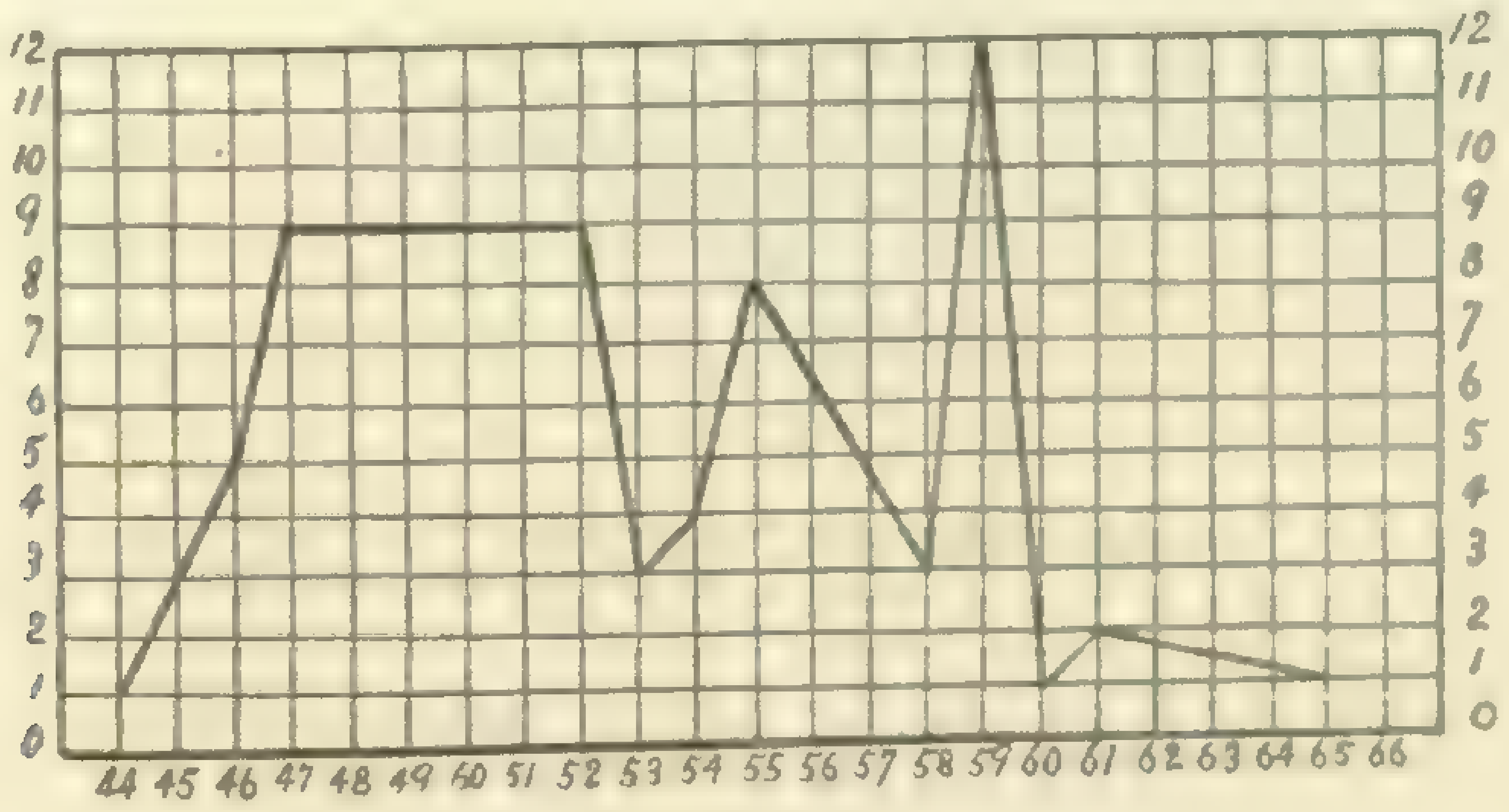

Fig. 1.— Rochester shells. Variation curve of 67 specimens.

peculiar aspect of this curve is the broad mode from 47 to 52 per cent., the frequencies being 9. The two sharp modes are 55 with a frequency of 8 and 59 with a frequency of 12. The variation is from 44 to 65 per cent. The data for Fig. 1 is shown in Table A.

Table A.

$\frac{44}{1}$	$\frac{46}{5}$	$\frac{47}{9}$	$\frac{50}{9}$	$\frac{52}{9}$	$\frac{53}{3}$	$\frac{54}{4}$	$\frac{55}{8}$	$\frac{58}{3}$	$\frac{59}{12}$	$\frac{60}{1}$	$\frac{61}{2}$	$\frac{65}{1}$

The number of shells examined was 67.

The Auburn Shells.

Figure 2.

The Auburn shells are not as variable as those from Rochester, a fact shown by the greater regularity of the curve, which

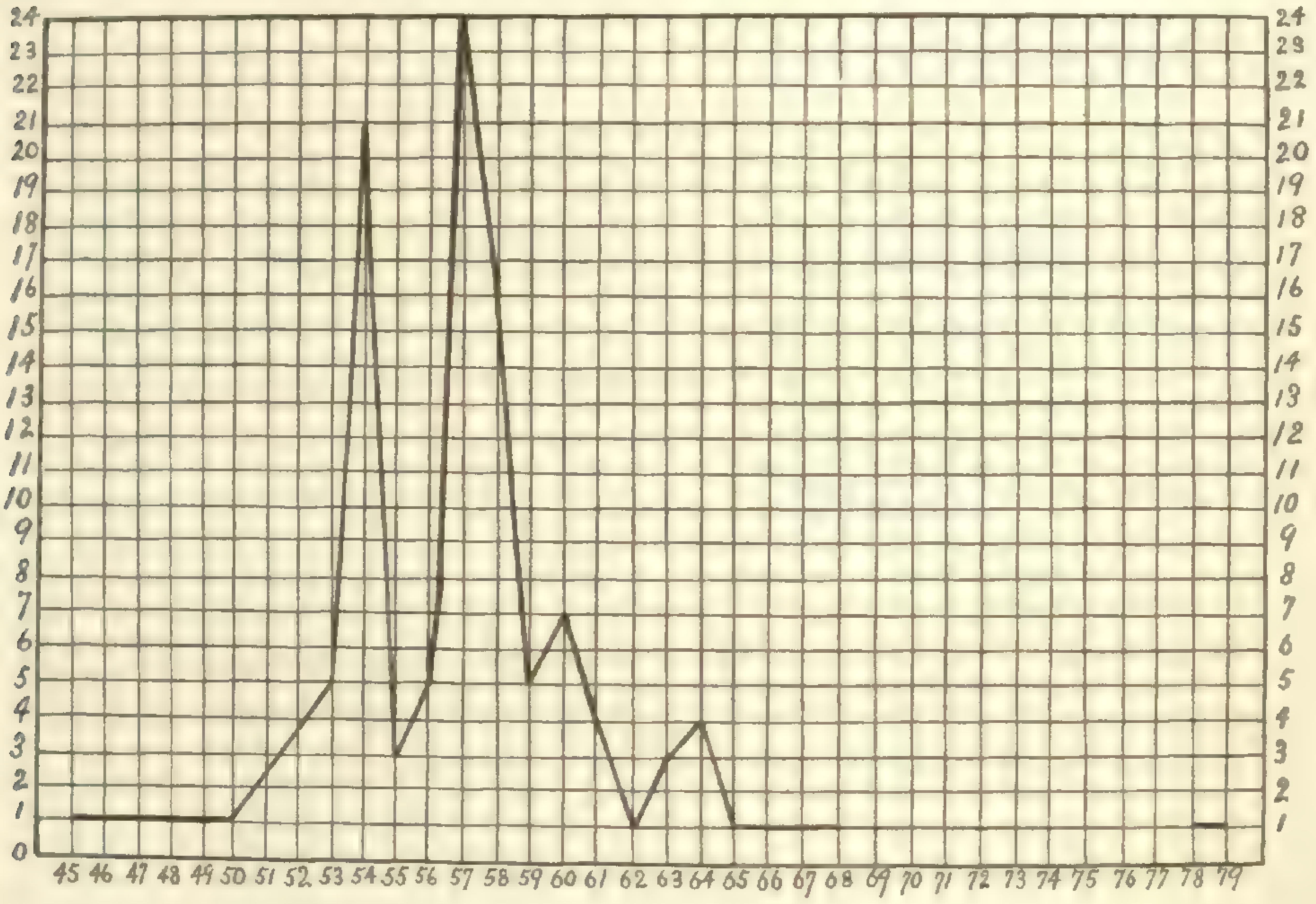

FIG. 2. — **Auburn shells. Variation curve of 104 specimens.**

is practically bimodal, the minor mode being at 54 per cent. with a frequency of 21 and the major mode at 57 with a frequency of 24. The data for this curve is shown in Table B.

Table B.

45	50	53	54	55	56	57	58	59	60	61	62	63	64	65	66	68	79
1	1	5	21	3	5	24	16	5	7	4	1	3	4	1	1	1	1

The number of shells examined was 104. The range of variation is from 45 to 79 per cent.

The Bowmanville Shells.

Figure 3.

The Bowmanville shells are the most variable of the three lots, the curve showing a marked multimodal tendency, which

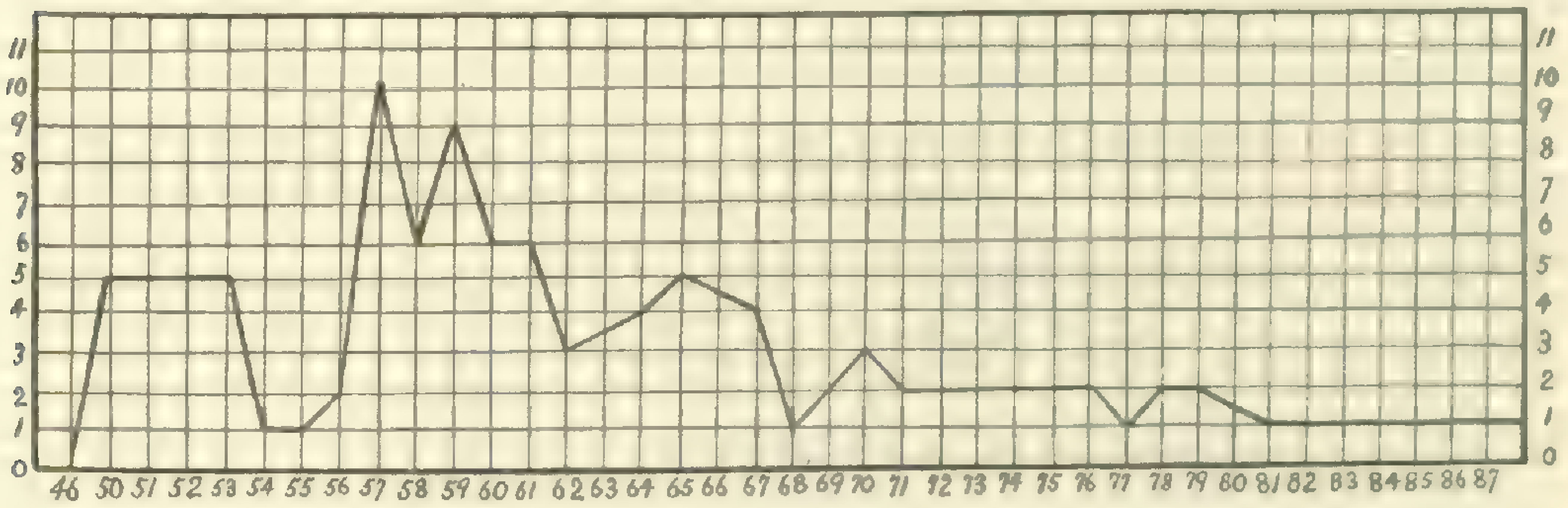

FIG. 3. — Bowmanville shells. Variation curve of 85 specimens.

always stands for extreme variability. The range of variation is from 46 to 87 per cent. There are four modes of prominence, at 50–53, 57, 59 and 65, with frequencies of 5, 10, 9 and 5, respectively. It will be noted that the curve for the Bowmanville shells is very similar to that of the curve for the Rochester shells, the peculiar broad mode being present in each. The data for this curve is shown in Table C.

Table C.

46	50	53	54	55	56	57	58	59	60	61	62	64
1	5	5	1	1	2	10	6	9	6	6	3	4
65	67	68	70	71	72	76	77	78	79	81	87.	
5	4	1	3	2	2	2	1	2	2	1	1	

The number of specimens examined was 85.

V. Comparison of the Three Localities.

Figure 4.

In comparing the three localities it will be noted that the Bowmanville and Rochester shells resemble each other very

closely in the form of their curves, which is quite different from

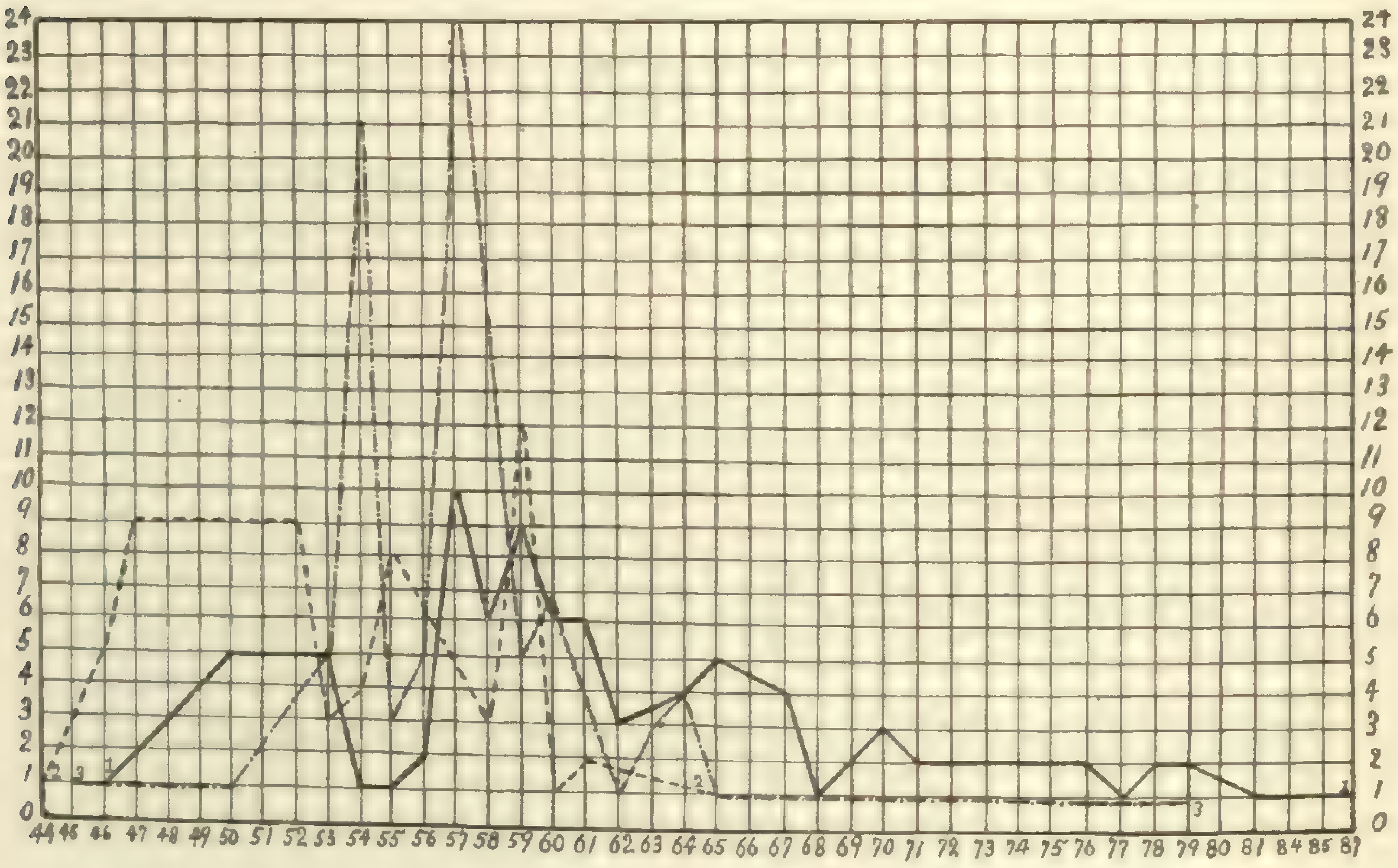

FIG. 4. — Comparison of the three localities. 1. Bowmanville. 2. Rochester. 3. Auburn.

the Auburn curve, which is very symmetrical, showing a smaller amount of variation. The major mode for the three localities is about the same, standing as follows:

Bowmanville	57%.[1]
Rochester	59%.
Auburn	57%.

The mean per cent. for the three localities is as follows:

Bowmanville	65.1%.
Auburn	59.7%.
Rochester	54.1%.

This shows that the Bowmanville shells have relatively the highest spires, while the Rochester shells have the lowest spires. The widest variation is found in the Bowmanville shells, where the extremes are 46 and 87 per cent.

[1] 100% would mean that the diameter and height were the same; hence the per cent. shows the relation of height to diameter.

Geographically the western shells show a wider range of variability than do the eastern shells. With one exception (Auburn 79%) the eastern shells have the per cent. of spire elevation between 44 and 68, while those from the west range between 46 and 87, the per cents. between 68 and 81 being numerous.

One of the most noticeable features in the curves as plotted in this paper is their tendency to assume a multimodal form. This is clearly shown in the individual diagrams, but stands out prominently in the comparison of the localities (Fig. 4). This is, of course, indicative of great variability.

From the study of these three lots of shells we may conclude that the western *alternata* has a higher shell, on the average, than does the eastern form, and that it shows a much larger amount of variation in spire elevation. It would be very interesting to have curves plotted from other localities, east and west, to ascertain whether their results would coincide with the conclusions of the present paper.

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The Chicago Academy of Sciences.
June 4, 1904.

FOSSIL PLUMAGE.

C. R. EASTMAN.

Preservation of avian remains in the fossil state is necessarily of very rare occurrence, and extraordinarily so, if fossilization takes place in marine sediments. Cases of the latter description presuppose the creature either to have perished at sea, or to have been swept out at a distance from the land as a floating carcass without having been destroyed by predaceous animals. The body must have sunk to the bottom before decomposition had advanced far enough to disrupt the skeleton and scatter the plumage. Burial by fine sediments must have followed almost immediately, in order that the body be preserved intact. And mineral replacement of the organic tissues must have proceeded in a wonderfully subtle manner, transforming the most delicate particles into stone without obliterating their microscopic structure.

Supposing a dead bird to have reached the bottom in a tolerably complete condition, the feathers naturally become loosened and scattered with decomposition of the skin, and the least current is liable to sweep them away except they become entangled and covered by the sediment at once. If the material happens to be a fine calcareous ooze, the feathers may leave in it an exceedingly delicate impression, or, in the rarest cases of all, their structure may become replaced molecule for molecule by mineral matter, generally calcareous or carbonaceous.

Chance, controlling thus absolutely the fate of this class of remains, goes away after sealing them up in the rocks to remain hidden for ages; but may peradventure come back again, and disclosing them to the light of day, permit them to fall into the domain of scientific investigation. Great as is the miracle, it has actually happened a few times, as witness the two complete individuals of Archæopteryx that are known, and one of Hesperornis, with their plumage preserved. Scarcely less

interesting and remarkable are the complete examples found in lacustrine and fluviatile deposits, the most perfect in our own country being Palæospiza from the insect-bearing shales of Florissant, Colorado, and Gallinuloides from the Green River Eocene of Wyoming. In the former the plumage is preserved, in the latter it is wanting.[1] Skeletons nearly as perfect as these have also been described from fresh-water deposits of the south of France and elsewhere in Europe.

But it is fossil plumage from marine deposits with which this article is especially concerned. The feathers of Archæopteryx are too well known to require more than a mere mention of their occurrence, and those of Hesperornis, recently made known from the Kansas Cretaceous, are still fresh in the minds of students.[2] There is yet another marine horizon from which feathers have been obtained, these constituting, however, the only indication of avian life which exists in the formation. This is the Upper Eocene limestone of Monte Bolca in the Veronese, famous for nearly four centuries on account of its remarkable fish and plant remains. But as for the occurrence of detached feathers to the exclusion of other remains, it should be remembered that marine and shore-birds are constantly shedding them, and hence, if circumstances favoring preservation are equal, they are likely to be numerically more abundant than bones.

Owing to their excessive rarity and wonderful preservation, it is not surprising that the few feathers thus far obtained from Monte Bolca should be objects of considerable interest. In the early days of palæontology, no little rivalry was created over the acquisition of the first specimens brought to light, one having been found in 1777, and another some twenty years later, both

[1] A solitary feather from the Green River shales of Wyoming was discovered by F. V. Hayden in 1869, and noticed by Marsh in the *American Journal of Science* for 1870 (vol. 49, p. 272). Detached feathers are also known from the Florissant locality in Colorado; the Lower Miocene of Ronzon, near Puy-en-Veday; the Upper Miocene lignite of Rott, near Bonn; and from the Upper Miocene lacustrine deposits of Oeningen, Switzerland. Good examples from the last-named locality, and of Ratite feathers from the Quaternary of New Zealand, are preserved in the Museum of Comparative Zoölogy at Cambridge.

[2] Williston, S. W., *Kansas Univ. Quar.* Vol. 5, p. 53, 1896.—Marsh, O. C., *Amer. Journ. Sci.* [4] vol. 3, p. 347, 1897.

being in counterpart. These two specimens, which are now preserved in the Paris Museum of Natural History, were described and figured in the early part of the last century by Faujas-St.-Fond,[1] but not without misgivings lest his readers be inclined to doubt their avian nature. The names are given of four professors at the Museum who agree with the author in his conclusions, and it is observed that with reference to one of the feathers, that "on ne sauroit la confondre avec certains *fucus* qui ont quelques rapports apparens avec des plumes, parce que celle-ci a ses barbes garnies d'autres petites barbes." This is the only statement which is given in regard to the finer structure, and the latter is not illustrated in the figures. Both of these feathers, it may be added, are of the pennaceous, and not of the plumulaceous variety.

Except for a casual mention by Milne Edwards[2] of his having seen one or two fossil feathers in Verona, where they are still on exhibition in the Public Museum, no other references occur in literature to this sort of remains from Monte Bolca. It may therefore be of interest to examine the figure which is given herewith of a specimen recently acquired by the Museum of Comparative Zoölogy at Cambridge, along with a fine suite of fish-remains from a famous old Veronese collection. This is a small contour feather, only 1.5 cm. long, but remarkable for its perfect preservation of details.

Fossil Carinate feather from the Upper Eocene of Monte Bolca, Italy. × $\frac{3}{1}$.

It is possible to distinguish each separate barb of the symmetrical vane, and even the barbules along either side of the branches.

[1] Faujas-Saint-Fond, B. Mémoire sur quelques fossiles rares de Vestena Nova dans le Véronais. *Ann. Mus. d'Hist. Nat.* vol. 3, pp. 18–24, 1804.

[2] Milne Edwards, A. *Oiseaux Fossiles de la France*, vol. II., p. 544, 1871.

The barbules appear relatively shorter, coarser, and less closely spaced than those in the body-feathers of recent Carinates, and the apex of the vexillum is more pointed. The shaft not being prolonged at the base, it is probable that the specimen is complete in itself, and not the tip of a larger feather. No inferences are warranted regarding even the remote affinities of the form it belonged to, beyond that chances favor its having been a shore bird of small or moderate size. Although the beds were undoubtedly laid down under deep-water conditions, the presence in them of crocodilians, chelonians, and plant remains indicates that the Bolca locality was not far removed from land at the time these strata were deposited. It deserves to be stated that, according to Walther, the Solnhofen lithographic stone in which Archæopteryx occurs was deposited within a coral island lagoon.

NOTES AND LITERATURE.

ZOÖLOGY.

"**An Introduction to Vertebrate Embryology**" by Dr A. M. Reese[1] is "the result of a need that the author has felt, for some years, for a concise text-book of embryology that described the development of both the chick and the frog" (Preface, p. v). It is questionable if such a need has been generally felt in the presence of existing treatises on embryology, though they may be more "cumbersome and expensive" books than Dr. Reese's. There is something to be said in favor of students becoming acquainted, at first hand, with standard works such as the text-books of Balfour, Hertwig, Marshall, and Minot.

To give a satisfactory account of the development of both the frog and chick within the space limits of a book like Dr. Reese's, the author must be a master of the subject and, equally important, he must be a master of the art of expression in written language. It is unfortunate that Dr. Reese's book does not do justice to its author's knowledge. The fundamental defect of the book — a defect which overshadows good qualities — lies in poor presentation of the subject, and, in a book which does not offer new material, form is the all-important thing, so long as facts are not violated. The account of the development of the optic nerve may be cited as an example of the quality of description. "It is sometimes stated that the *optic nerve* is formed by the hollow stalk of the optic cup; but it is probable that it is formed by an outgrowth of cells from the retina, this outgrowth extending along the optic stalk to the brain, and forming the fibres of the optic nerve. The growth of these fibres may have, as has been mentioned, something to do with the formation of the choroid fissure" (p. 181). What, in the light of this paragraph, is the manner of development of optic nerve fibres? The account of the development of the chick begins with the sentence, "The egg of the chick (Fig. 33) is of large size, ovoid in shape and usually some-

[1] Reese, A. M. *An Introduction to Vertebrate Embryology Based on the Study of the Frog and the Chick.* New York, G. P. Putnam's Sons, 1904. XVII + 291 pp., 84 figures.

what larger at one end than at the other" (p. 90). (If the egg of the "chick" were not ovoid, what would its form be?) Then follows what apparently is a description of the egg at the time of laying. In the course of this description it is stated that the yolk exhibits on one side "a small, whitish circle, the *blastoderm* or *cicatricula*" (p. 91). The next paragraph tells us that "Although of so large a size, the yolk of the hen's egg is a single cell, its great size being chiefly due to the large number of yolk granules which it contains "(p. 92). Fortunately, the last paragraph of the section on "The Egg" explains, as if by an afterthought, that "The preceding is a description of the egg at the time of its laying" and that "The statement that the yolk is a single cell is really true only from the time it leaves the ovary until it is fertilized, or until a short time after fertilization, when segmentation begins" (p. 93). Even then we are left in doubt as to the precise time when the egg ceases to be a single cell. It does not tend toward conciseness to make an incorrect statement and then add a paragraph to explain what is "really true."

In the accounts of the visceral apparatus of both frog and chick, an indiscriminate use of the terms *gill*, *branchial*, and *visceral*, as applied to the several arches and clefts, leads to hopeless confusion. It is doubtless by an oversight that the author states that the ectodermal auditory invagination of the frog gives rise to the lining of the middle ear (p. 43). It is a surprise to find the terms *somatopleure* and *splanchnopleure* applied to the parietal and visceral layers of mesoderm respectively. The use of the incorrect plurals "diverticulæ" and "lumena," an apparent failure to appreciate that *nares* is a plural, and reference to nascent organs as rudiments are comparatively unimportant matters. The figures, mainly from Marshall, Duval, and Minot, are well reproduced, but their arrangement in relation to the text could be much more convenient.

A book such as Dr. Reese has proposed should lay down in a few firm bold strokes the main outlines of the subject. Unimportant details should be omitted, important details must be adequately treated. The account must proceed in an orderly constructive way, always complete so far as it has progressed, like the development it portrays. There must be such unfailing accuracy and such clearness of statement that misconception is impossible. If Dr. Reese's book is not an unqualified success, it is because the author undertook a very difficult task.

H. W. R.

A Hermit's Wild Friends.[1]— The first impulse of a reviewer on reading this book is to rage and to utter vain things. There is something peculiarly irritating in the cock-sureness and the condescension of ignorance; there mingles, no doubt, with our zeal for the defense of truth a little of the wrath of the orthodox prophet against him who would lead the people after false gods and therefore after a false prophet. If it were only a question of the scientific world, it would be hardly necessary to pay any attention to the book, but the reviews quoted by the publishers show how easily the general press are mislead. The Hermit is hailed as a second Thoreau, or put before Thoreau, since he "spares us Thoreau's philosophy." One reviewer admits that there is much "out-of-the-way information," but is convinced that it all bears "the stamp of truth." Another reviewer assures us gravely that the book never goes "beyond the observed facts." It is rather against an unscrupulous publisher and irresponsible reviewers that our wrath should be directed; the Hermit's sins are those of ignorance and vanity; the publisher's are those of greed.

The book purports to give true and detailed records of intimacies with wild animals of the Gloucester woods, where the author has lived for years. He has numbered among his intimates, song sparrows, chewinks and chickadees, squirrels, mice and crows. It will only be necessary to give an extract taken almost at random to show the character of the book. The "Hermit" has found (p. 187) a crippled sparrow and has been feeding him in his camp in the woods. "The fourth day, while I was feeding him, an old chewink hopped to the loaf of bread [always put out for the birds], and called him. The sparrow did not respond at first, but after awhile hopped over to see what the chewink wanted. He seemed surprised to find the bread, and began at once to help himself. The chewink called him into the bushes. *I suppose he intended to give him an introduction to his family.* The next day the sparrow came into the dooryard alone. He made for the bread and did not look at me. I tried to catch him, but he hopped into the bushes, apparently filled with terror. I think that old chewink had told the sparrow that I was a very bad man. The old fellow might have been jealous, and had frightened the young sparrow, so that he would fly from me in wild alarm. The next time the sparrow visited the yard the

[1] Walton, Mason A. *A Hermit's Wild Friends.* Boston, Dana Estes & Co. [1903]. pp. 1–304.

chewink was with him. They departed together, and three days later I saw the sparrow near the old barn. . . . . *It was evident* that the chewink had piloted him three-fourths of a mile to his friends. . . . . How did the chewink know where to take the sparrow?" How indeed? The italics are the reviewer's and this passage is commended to the critic who could say that the book never went "beyond assured facts." When we add that the illustrations are in keeping with the text we have done all that is possible to put the public on their guard against this book.

R. H.

The Sino-Australian Continent.—The existence of this continent, first assumed by Neumayr for the Jurassic period, and which was accepted by various subsequent writers for the Cretaceous, and upward in the geological scale to the beginning of the Tertiary, apparently needs restriction with regard to its duration. It now is rendered more or less probable that it was not present at all in the Jurassic period. Lately G. Bœhm[1] has demonstrated that, in the region of the Moluccas, Mesozoic marine deposits of European type are largely developed, and are chiefly represented by various horizons of the Jurassic series. Bœhm draws the conclusion, "it becomes apparent that a Sino-Australian Jurassic continent, as conceived by Neumayr, did not exist."

On the other side, deposits of Cretaceous age are absent or scarce in this region. so that this old continent might have existed at least during a part of the Cretaceous period. Bœhm does not discuss this question, but we must bear in mind that zoögeographical facts positively demand a connection of Australia with eastern Asia, and all evidence tends to show (see H. von Ihering, C. Hadley. H. A. Pilsbry, A. E. Ortmann, M. Weber) that this connection was a broad and important one in pre-Tertiary times, while, during the Tertiary, it became more irregular, and was subject to many changes which amounted frequently to complete interruption, which latter condition prevails at present. The restriction of the Sino-Australian continent to a certain part of the Cretaceous times consequently would meet the postulates both of geology and zoögeography.

A. E. O.

[1] Geologische Ergebnisse einer Reise in den Molukken, in: *Compt. Rend. 9. Congr. Geol.*, Wien., 1904.

Origin of the Large Mammals of North America.—M. Grant[1] discusses the old continental connections of North America with the Old World and with South America. Most important is his idea about the old "Beringian connection" between northeastern Asia and northwestern America, which, according to him, was not a continuous one in time, as generally accepted (from the upper Cretaceous to the lower Pleistocene). Grant believes that it existed in the lower Eocene, lower Oligocene, middle Miocene, upper Pliocene and lower Pleistocene, but that it was interrupted chiefly in the middle and upper Eocene, upper Oligocene and lower Miocene. The evidence supporting this assumption is not very convincing, since in part it may be founded only upon a deficiency in our knowledge of the fossil Mammals both of the Old and the New World. Moreover, the geographical distribution of marine animals does not support this view, at least as far as it refers to the older Tertiary. There is hardly any trace of an exchange of faunas between the northern Pacific and the northern Atlantic by way of the Arctic basin during earlier Tertiary times, the similarities in the faunas of these oceans generally being clearly indicative of a very recent connection of them. There is either no resemblance at all, or very close affinity of forms generally amounting to specific identity, the latter cases being found among forms that are apparently circumpolar cold-water types of recent origin.

It shall not be denied that there are a few cases of allied or even identical species in both oceans belonging to more temperate climatic conditions (for instance, resemblances of Japanese and Mediterranean forms) which might possibly indicate a former interruption of the Beringian bridge in the beginning of the later half of the Tertiary, but this point needs further elucidation.

A. E. O.

PALÆONTOLOGY.

Walther's Solnhofen Fauna.[2] — One of the most philosophical discussions of extinct Faunæ is this essay by Dr. Walther, which forms part of the Hæckel Anniversary Volume. The geological

[1] *8th Ann. Rep. New York Zool. Soc.*, 1904.

[2] Walther, J. *Die Fauna der Solnhofener Plattenkalke, bionomisch betrachtet.* Jena. 1904.

evidence is interpreted as demonstrating the extension of coral reefs throughout the shallow sea covering Central Europe in late Jurassic time, which was a period of oscillation. The fine calcareous sediment interbedded with lithographic stone, for which the district about Solnhofen is famous, represents the infilling of a lagoon, outside of which the coral limestone carries a totally distinct fauna. The peculiar mixture of land and marine organisms, the occurrence of large trunks of trees and seaweed with roots, the interbedding of apparently wind-blown material, and the tracks of undoubted air-breathing animals, are among the facts which indicate that the bottom of the lagoon was barely below tidewater, and probably was even exposed at times. Creatures straying into the lagoon and becoming entrapped there, or volant forms like insects, Pterodactyls and Archæopteryx, which met their death in the paste-like, rapidly accumulating sediment, were covered before any injury had been done to their bodies through decomposition or other causes, the most delicate structures being perfectly preserved. Although the variety of forms is large, yet Solnhofen fossils are surprisingly rare as compared with the majority of horizons, and a great many species are known only by one or two individuals; several important groups are not represented at all, and on the other hand, a large percentage of species is restricted to this locality. There appears to be no room for doubting that the assemblage is an accidental one, and this vast cemetery gives us a unique but by no means typical reconstruction of the late Jurassic fauna.

Karl Alfred von Zittel.— Of the numerous biographical sketches which have appeared of the great master of palæontology this recent memorial of Pompeckj, pupil, associate and intimate friend of the late Geheimrath, is the most complete, and most satisfactory. This is not a eulogy of von Zittel, but a plain and sufficient account of his career, with his achievements mentioned in such a way that they speak for themselves, and with the light so distributed upon his personal traits, his ambition, energy, concentration — and above all upon his aptitude as a teacher, helpful, inspiring and commanding of respect,— that his character is revealed naturally before us without addition or subtraction, as must be acknowledged by anyone who had the good fortune to know him well. Dr. Pompeckj has told us

[1] Pompeckj, J. F. Karl Alfred von Zittel: Ein Nachruf. *Palæontographica*, vol. L., 1904.

in measured and dignified language much that is good to know and to remember in connection with the life-work of one of the torch-bearers of science, but there is one respect in which we would like to have been told more. Zittel as a teacher, text-book writer, ardent collector and museum administrator, Zittel as an investigator thirsting for scientific discovery — in all these capacities he is presented to us ; but enough has not yet been said in regard to him as a philosopher, as a theorizer upon the vast store of empirical knowledge of which he was the possessor. He was an excellent systematist, and the faculty of coördination was developed in him to a remarkable degree. Though he discovered no new laws of natural history, yet he had faith in the discovery of others, and he believed in certain principles and methods of drawing philosophical conclusions, as sincerely as he disbelieved in certain others, nor did he always insist upon his own personal judgment, often deferring to the opinions of colleagues in whom he had confidence. On such matters as these we should eagerly welcome more light.

BOTANY.

Maple Sap Flow.[1]— This paper, by Messrs. Jones, Edson, and Moore, and edited by J. H. Hills, Director of the Agricultural Experiment Station of Vermont, is unusual in two ways. It is a very good paper, giving the carefully considered results of experiment and observation sufficiently extended to justify general conclusions. In the second place the paper is unusual for it is the first on this subject since Clark's papers in 1873 and 1874.[2] As I have said elsewhere,[3] it is surprising that American botanists at the Agricultural Experiment Stations in the states where maple-syrup and maple-sugar making is an important industry have not carefully studied the phenomena, at least from an economic standpoint. The present paper is written both from the economic and from the physiological standpoint, and the plant physiologist will find in it data which he

[1] *Bulletin Vermont Agric. Exp. Station*, No. 103, Dec., 1903.

[2] *Report Mass. Agric. Coll.*, 1873–4 ; *Report Mass. State Bd. Agric.*, No. 22, 1874.

[3] *Text Book of Plant Physiology*, 1903.

has long wished to have. The paper is of such length (184 pages, 8vo) that even an abstract may easily be too long for this journal.

After an introduction, stating the importance of the maple-sugar industry, the process of sugar-making, and former investigations, the authors proceed to describe their plan of work and the scope of their investigations. A few pages are given to the structure and general physiology of the maple. In sixty pages the authors discuss (1) the water and gas contents of the maple at different seasons, comparing it with other trees; (2) pressure, positive and negative, at different seasons, in different parts of the tree, and the direction of pressure and sap movement; (3) temperatures, comparing internal with external. It is to be hoped that this study of external temperatures will be supplemented by further ones. The authors studied only air temperatures, but it is obvious that the temperatures of the soil must have at least an equal, if not a greater, bearing on the phenomena of sap flow in the spring than the air temperatures. As others have shown, the roots begin to be active much earlier than the aërial parts of trees and shrubs growing in the temperate zóne. This early resumption of active life in the roots, and the energetic absorption of water from the soil, depend more directly on soil temperatures than on air temperatures. Hence, if we are thoroughly to understand the process of periodic sap flow, we must know all the conditions, not merely those in the air and in the aërial parts of a tree. It may not be too much to suggest also that studies of the water-content of soil and air before, during, and after sugaring time would be a valuable addition. This is intimated by the authors, though the subject is not pursued further.

The remaining seventy pages are occupied by a discussion of economic problems and by tabular reports of weather conditions, etc.

G. J. P.

The Journals.— *The Botanical Gazette*, May:— Sargant, "The Evolution of Monocotyledons"; Smith, "The Nutrition of the Egg in Zamia"; Opperman, "A Contribution to the Life History of Aster"; Cardot and Thériot, "New or Unrecorded Mosses of North America"; Livingston, "Physical Properties of Bog Water"; Rose, "William M. Canby"; Ramaley, "Anatomy of Cotyledons."

The Bryologist, May:—Grout, "The Peristome—VI"; Holzinger, *Rhacomitrium Flettii*, n. sp."; Holzinger, "A Bryologist's Glimpse into Geological History"; Harris, "Lichens—Collema and Lepto-

gium"; E. G. Britton, "Notes on Nomenclature — III"; Grout, "The Specific (?) Value of the Position of the Reproductive Organs in Bryum"; and a number of short notes by various persons.

The Fern Bulletin, April: — Curtiss, "The Fern Flora of Florida"; Eaton, "The Genus Equisetum in North America—XVII"; Clute, "New or Rare Ferns from the Southwest"; Eaton, "Preliminary list of Pteridophyta Collected in Dade Co., Florida, during November and December, 1903"; Kalbfleisch, "*Polystichum acrostichoides* and some Insects that infest it"; Burnham, "Ferns of Ann Arbor, Mich."; Clute, "Raynal Dodge" (with portrait); and short notes by various persons.

Journal of Mycology, March: — Morgan, "A New Melogramma"; Cockerell, "Some Fungi Collected in New Mexico"; Dudley and Thompson, "Notes on Californian Uredineæ and Descriptions of New Species"; Kellerman, "Ohio Fungi, Fascicle IX"; Kellerman, "Minor Mycological Notes — III"; Kellerman, "Index to Uredineous Culture Experiments, with List of Species and Hosts for North America — I" (concluded); Kellerman, "Notes from Mycological Literature—IX"; and Kellerman, "Elementary Mycology."

Journal of the New York Botanical Garden, May:—MacDougal, "Botanical Explorations in the Southwest"; Broadhurst, "The Protection of Our Native Plants."

The Ohio Naturalist, May: —Claasen, "List of the Mosses of Cuyahoga and Other Counties of Northern Ohio"; and Schaffner, "Deciduous Leaves."

The Plant World, April: — Safford, "Extracts from the Note Book of a Naturalist on the Island of Guam — XVII"; Broadhurst, "Nature Study as a Training for Life"; Nehrling, "The Beginning of Spring in Florida — I."

The Plant World, May: — Morris, "The Bush Morning Glory"; Safford, "Extracts from the Note Book of a Naturalist on the Island of Guam — XVIII"; Nehrling, "The Beginning of Spring in Florida—II."

Rhodora, May: — Parlin, "Some Casual Elements in the Flora of Western Maine"; Pease, "Preliminary Lists of New England Plants—XV"; Sanford, "Occurrence of *Verbena stricta* and *Helianthus mollis* in Mass."; Hill, "Note on the Polygamy of Chionanthus"; Woodward, "Two Noteworthy Plants of New Haven, Ct.";

Robinson, "*Stellaria glauca* established in the Province of Quebec"; Knight, "Some Plants New to the Flora of Maine"; and Eaton, "Note on *Equisetum pratense.*"

Proceedings of the Society for the Promotion of Agricultural Science, Vol. 25: — Hansen, "Possibilities of the Western Sand Cherry"; Pammel, "Some Unusual Fungus Diseases in Iowa during the Summer of 1903"; King, "Promising Methods for the Investigation of Problems of Soil and Plant Physiology, and Some Lines of Investigation to which they are Adapted."

Bulletin of the Torrey Botanical Club, April: — Peck, "New Species of Fungi"; Evans, "Hepaticæ of Puerto Rico — IV"; Morgan, "Polarity and Regeneration in Plants."

Bulletin of the Torrey Botanical Club, May: — Nelson, "New Plants from Wyoming — XV"; "Code of Botanical Nomenclature" (in three languages); Watterson, "The Effect of Chemical Irritation on the Respiration of Fungi."

Torreya, April:—Underwood, "Early Writers on Ferns and their Collections— II"; Rusby, "William Marriott Canby"; MacKenzie, "Notes on Evening Primroses"; Cockerell, "Mutations and Ferns"; Sumstine, "A New Hydnum."

Torreya, May: — Eggleston, "A Canoe Trip on the St. Francis River, Northern Maine"; Kobbé, "Notes on the Local Flora"; and Britton, "*Viburnum molle* Michx."

Zoe, April: — Brandegee, "A Collection of Mexican Plants"; Greenman, "New Species of Mexican Plants"; T. S. Brandegee, "Palms of Baja California"; and Katharine Brandegee, "Notes on Cacteæ."

Notes. — A "Flora of Los Angeles and Vicinity," by Abrams (Stanford University Press, April 5, 1904) forms an octavo volume of 474 pages, and contains analytical keys and full descriptions of the Spermatophyta of the coast slope of Los Angeles and Orange Counties, California. The Orders are arranged in the Engler and Prantl sequence, and the Neo-American nomenclature is adopted — with synonymic citation where the generic name is unfamiliar to the ordinary reader.

A Catalogue of the Bryophyta and Pteridophyta of Pennsylvania, by the late Professor Porter, edited by Dr. Small (Boston, Ginn &

Co., 1904) forms an octavo of 66 pages. Each entry is followed by habitat and distribution data by counties.

A check-list of the higher plants of Hamilton County, Ohio, and a list of medicinal plants growing in the vicinity of Cincinnati, both by Aiken, form no. 4 of Vol. 20 of the *Journal of the Cincinnati Society of Natural History*.

A few separates of the several chapters of Vol. 5 of the publications of the Harriman Alaska Expedition, dealing with the cryptogams, have been distributed by the authors.

A dictionary of plant names of the Philippine Islands, by Merrill, forms a bulletin from the Philippine Bureau of Government Laboratories.

A paper on the flora of St. Andrews, New Brunswick, by Fowler, is published in "Contributions to Canadian Biology," — a supplement to the 32d *Annual Report of the Department of Marine and Fisheries, Fisheries Branch*, of Canada.

Fascicle 2 of Millspaugh's "Plantæ Yucatanæ," forming Vol. 3, no. 2, of the botanical series of *Publications of the Field Columbian Museum*, deals with Compositæ, by C. F. Millspaugh and Agnes Chase, and is admirably illustrated.

The first fascicle of Vol. 3 of Halacsy's "Conspectus Floræ Græcæ," recently issued, covers Lentibulariaceæ to part of Cyperaceæ.

A general comparison of the Alpine floras of Australia and Europe is given by Weindorfer in *The Victorian Naturalist* of September last.

Forbes and Hemsley's enumeration of the plants of China, etc., forming Vol. 36 of the *Journal of the Linnean Society* (Botany), has reached the 18th part, dealing with parts of Cyperaceæ and Gramineæ.

Warburg and de Wildeman have begun the publication of an account of Ficus as represented in the Congo district, in the *Annales du Musée du Congo*, the first fascicle being issued in January, 1904.

The newly established *Records of the Albany Museum*, of Grahamstown, is in part devoted to South African botany.

Part 10 of Hough's *American Woods*, comprising nos. 226 to 250, represents chiefly western and southwestern species, — perhaps the

most interesting being *Cereus giganteus*. Like earlier fascicles, this is accompanied by leaf and fruit keys and indexes for the entire issue, and a systematic account of the species now distributed.

An excellent winter key to the genera of woody plants, wild or cultivated, in New York State has been issued by Wiegand and Foxworthy, of Cornell University.

A polyglot Code of Botanical Nomenclature, by a committee of the Botanical Club of the American Association for the Advancement of Science, has been separately printed from the May *Bulletin of the Torrey Botanical Club*.

The sixth fascicle of Dalla Torre and Harms' "Genera Siphonogamarum" includes Gentianaceæ (in part) to Acanthaceæ (in part), — genera 6492–7927.

The roses of Pecos, N. M., are discussed by Cockerell in Vol. 56, part 1, of the *Proceedings of the Academy of Natural Sciences of Philadelphia*.

Figures of *Jamesia Americana* are published by Späth in *Gartenflora* of May 1.

A paper on Echeveria, by Berger, is published in *Gartenflora* of April 15.

Professor Greene contributes a paper on Some Canadian Antennaries to *The Ottawa Naturalist* for May.

Gaylussacia resinosa is figured in Vol. 4, fascicle 7, of *Icones Selectæ Horti Thenensis*.

Abronia is recorded for the Tertiary flora of Europe by Laurent in the *Comptes Rendus* of the French Academy, of April 18.

Kraenzlin's "Orchidacearum Genera et Species," which had reached the end of Part I of Volume 2, has been broken off.

Several tropical American orchids are added to the known flora of Florida by Ames in a leaflet of Vol. 17 of the *Proceedings of the Biological Society of Washington*, issued May 19th.

An interesting article by Miller on cultivated orchids, well illustrated, is contained in *Country Life in America* for June.

A preliminary synopsis of the Southern California Cyperaceæ, by Parish, is in course of publication in the *Bulletin of the Southern California Academy of Sciences*.

The leaf characters of Pinus are discussed by Masters in No. 248 of *The Journal of the Linnean Society, Botany.*

An important paper on ferns of central China, by Christ, is published in No. 173 of the *Bulletin de l'Académie Internationale de Géographie Botanique.*

An account of the liverworts found about Chapel Hill, N. C., is given by Coker in the January *Journal of the Elisha Mitchell Scientific Society.*

Part 2 of Grout's "Mosses with Hand Lens and Microscope" was issued in May, and extends from Ceratodon to Tortula.

A list of the lichens and mosses of Montana, by W. P. and C. W. Harris, forms *Bulletin No. 7, Biological Series*, of the University of Montana.

An account of the diatoms of the Gulf of Naples, by Balsamo, is being published in the *Bollettino della Società di Naturalisti in Napoli.*

A study of the plankton of Lake Winnebago and Green Lake, by Marsh, forms *Bulletin 12* of the Wisconsin Geological and Natural History Survey.

A monographic account of *Triphragmium*, by Milesi and Traverso, is published in *Annales Mycologici*, of March.

An illustrated account of *Stictis Panizzei*, and its disease of the olive, is given by Brizi in *L'Italia Agricola* of April 15.

An account of *Colletotrichum glæosporioides* and its diseases of Citrus is published by Rolfs as *Bulletin 52* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

The report of the botanist of the Connecticut Agricultural Experiment Station for 1903 is devoted to diseases of plants cultivated in that State, and the inducing fungi.

Fungous diseases of fruits in Michigan are discussed by Longyear in *Special Bulletin No. 25* of the Experiment Station of that State.

The fungous parasites of Hevea form the subject of No. 34 of the *Notizblatt des k. botanischen Gartens und Museums zu Berlin*, by Hennings.

An exhaustive paper on the yeasts which ferment milk-sugar, by Heinze and Cohn, is published in the *Zeitschrift für Hygiene und Infectionskrankheiten* of March 31.

Popular resumées of the plants used for various economic purposes are being published by Lagermann in current numbers of the *Journal of the Columbus Horticultural Society.*

The use of plants in controlling and reclaiming sand-dunes is considered by Hitchcock in *Bulletin 57* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

A paper by Sherman on gutta percha and rubber of the Philippine Islands is published as a bulletin from the chemical laboratory of the Bureau of Government Laboratories of the Philippines.

An account of *Senecio jacobœa* as the causative agent of hepatic cirrhosis of horses and cattle, is contained in the *Annual Report of the Department of Agriculture of New Zealand*, for 1903.

An economic account of annual flowering plants, by Corbett, is published as *Farmers' Bulletin No. 195* of the U. S. Department of Agriculture.

An economic account of the date palm, by Swingle, forms *Bulletin 53* of the Bureau of plant industry of the United States Department of Agriculture.

Noriega contrasts true and false Jalap in Vol. 6, No. 3, of the *Anales del Instituto Médico Nacional* of Mexico.

An account of poison ivy is contributed by Brownell to *Country Life in America* for June.

A readable account of English herbals, by Agnes Robertson, is contained in the *Popular Science Monthly*, for May.

One of the most suggestive of recent horticultural books is "The Tree Doctor," by John Davey (Akron, Ohio).

An important paper on root trichomes of Pteridophytes and Angiosperms, by Leavitt, constitutes Vol. 31, No. 7, of the *Proceedings of the Boston Society of Natural History.*

A paper by Hus, on spindle formation in the pollen-mother-cells of *Cassia tomentosa*, forms the concluding number of Vol. 2 of the third series of *Proceedings of the California Academy of Sciences, Botany.*

Deformation of plants through external influences is discussed by Reinke in the *Botanische Zeitung*, Abtheilung 1, of May 1.

The connection of leaf structure and environment, in *Pteris aquilina*, is considered by Boodle in No. 248 of *The Journal of the Linnean Society, Botany.*

Popular botanizing has received an admirable aid in Miss Niles's "Bog-trotting for Orchids" (New York, G. P. Putnam's Sons, 1904), a book for lovers of the country, written by a nature lover, in which is included a compiled synopsis of the orchids of New England. Plain and tricolor half-tones in large number are interleaved with the text.

An illustrated account of the botanical garden of Carlsaue (1580), the first of its class in Germany, is published by Junge in *Gartenflora* of April 1.

A biographic sketch of Askenasy, with portrait, appears in the *Berichte der deutschen botanischen Gesellschaft* of April 11.

A portrait of Professor Rothrock is contained in *Forestry and Irrigation* for May.

A biographic sketch of Karl Schumann, with portrait, is contained in the April *Monatsschrift für Kakteenkunde.*

CORRESPONDENCE.

To the Editor of the American Naturalist:

SIR: — Apropos of Dr. Theodore Gill's letter in the March number relative to early collections of the vernacular names of animals, it is interesting to recall that Thomas Gray, "the English poet who has written less and pleased more than any other," was an accomplished naturalist for his time, and busied himself during the last ten years of his life in compiling, amongst other notes, a voluminous catalogue of the familiar names of plants and animals. Not only the common English synonyms are given of Linné's species, but also their equivalents in more than a score of languages, some of the citations being from remote and little-known tongues.

These lists were written down by Gray in his interleaved copy of the tenth edition of the *Systema Naturæ*, and portions of them, some 25 pages in all, were published in the second volume of Mr. T. J. Mathias's edition of Gray's *Works*, which appeared in 1814. Other selections from the same source, with facsimiles of some of his drawings, have recently been published by Mr. Charles Eliot Norton, who now possesses Gray's original copy. No one can take up this little booklet [1] without feeling grateful to Professor Norton for having placed this "monument of Gray's learning and industry" within general reach. It is stated by the editor that these annotations, if printed, would form a volume at least equal in size to one of Linné's, and that the light they throw on the poet's occupations and interests during his latter years helps us to a "more just appreciation of his character and his acquisitions."

Those interested in the derivation of the common names of animals may find it worth while to consult a paper by J. W. Gibbs on the "Origin of the Names of Beasts, Birds, and Insects," published in vol. xli, of the *American Journal of Science* (pp. 32–39, 1841).

C. R. EASTMAN.

[1] *The Poet Gray as a Naturalist with Selections from his Notes on the Systema Naturæ of Linnæus* etc. Boston, Charles E. Goodspeed. 1903. pp. 67.

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THE ANATOMY OF THE CONIFERALES.

D. P. PENHALLOW.

(*Continued from page 554.*)

RESIN PASSAGES.

Distribution and Taxonomic Value.

PRANTL (44, p. 37) states that resin passages occur in the wood of "most Abietineæ, namely, Pseudotsuga, Picea, Larix, Pinus and *Abies firma*." This statement requires some modification in detail, especially with respect to the last named genus, and in order to make the results of the present studies clear it will be expedient to discuss separately the distribution of the resin cysts and the resin passages.

The first species to which our attention may be directed is *Tsuga mertensiana*. This is the only species of the genus in which definite resin cysts are to be found. Such structures are never numerous, and they take the form of short rows of contiguous cysts in the initial layer of the summer wood of distant growth rings. Longitudinally they have no definite limits, but they appear to be extended for great distances, and probably

through the entire longitudinal growth of the season, at least. There is no obvious alteration either in the position or volume of the resinous contents of the isolated resin cells which lie on the outer face of the summer wood. The constancy with which these structures occur gives to them a definite value for the recognition of the species, and permits us to differentiate it from *T. caroliniana* on the one hand and from the remaining three species on the other.

In the genus Abies only four species out of eleven show resin cysts. These are *A. bracteata*, *A. nobilis*, *A. concolor* and *A. firma*. Referring again to Prantl's observation (44, p. 37), it must be pointed out that his statement with respect to the occurrence of resin passages in *A. firma* requires modification in detail, in so far as these structures are not passages but cysts; while he also appears to have overlooked the occurrence of similar structures in the three other species mentioned. In all of these cases the cysts are contiguous and disposed in tangential rows of considerable length, either in the summer wood (*A. concolor* and *A. nobilis*), in the outer spring wood (*A. firma*), or in both the spring and summer wood (*A. bracteata*). Such variations appear to be of no specific value, conforming as they do to similar variations in the zonate distribution of the resin cells. It is found, however, that in only one case (*A. concolor*) are these cysts associated with isolated resin cells. In the three other cases the resin cells are entirely wanting, a relation which is strongly suggestive of their replacement by the cysts.

Sequoia sempervirens is the only species of that genus which develops resin cysts in the secondary wood, though Jeffrey (24) has shown that such structures are normal to the primary wood zone of *S. gigantea*, and not elsewhere. As already shown, such cysts are much more highly organized than those of either Tsuga or Abies, though they are similarly contiguous and even coalescent, and form extensive tangential rows in the initial layer of the spring wood of distant growth rings. They form a much more prominent feature than in any of the preceding species, because of their generally larger size and the greater extent of the series in which they lie. Unlike Abies, however, there appears to be no diminution either in the number or the extent

of the prominent resin cells which are often intimately associated with the cysts.

The normal course of development for such cysts as thus described is subject to special alteration under conditions which involve an unusual stimulus to growth, and under such circumstances they may become definitely associated with, or may even be regarded as indicative of, pathological conditions. Thus Anderson (1, p. 28–29) has shown that such cysts are definitely developed in association with the formation of Witches' brooms in *Abies firma*. Under such circumstances the cysts become much larger, more distant and more numerous than in normal growth, but they form well defined tangential rows in the earlier spring wood of successive growth rings. In the development of such secondary features the cysts manifestly exhibit a distinct approach to that higher type of structure and distribution which is exhibited in Picea. In the following year Anderson (2, p. 336) further showed that while resin cysts are absent from the normal wood of *A. balsamea* they do arise under the influence of the special stimulus connected with the formation of tumors produced by the action of *Æcidium elatinum*. He furthermore points out that such cysts attain their greatest development and largest number in the region of greatest stimulation, *i. e.*, in the middle of the tumor, decreasing above and below until they eventually become pointed and finally disappear between four tracheids "which, in their meristematic condition, probably function as epithelial cells." It is unfortunate that the histological details of these cysts and their endings are not given, since such facts would serve to throw much light upon the relation of the cysts to similar structures in normal tissues, but there is no reason to suppose that they differ in their essential structure from those which occur in the normal tissues of the same or other species. The tracheids above referred to are undoubtedly parenchyma tracheids, and it is probable that further examination would show that they ultimately replace the resin cells remaining over after the disappearance of the cyst proper.

More recently Jeffrey (24) has contributed an important paper on the anatomy of Sequoia in which he brings out several facts of considerable value. He shows that resin cysts may

arise in the roots of *Abies balsamea* which have been injured, while they may also be produced experimentally by injury, thus confirming the observations of Anderson that they may be traumatic in their origin. The most significant facts, however, relate to the normal occurrence of such cysts in Sequoia. He shows in the first instance that they are absent from the wood of the first year's growth in *Sequoia sempervirens*, while they are present for the same period of growth in *S. gigantea*, though absent from the growth of later years. In both species they arise in the earlier spring wood. Jeffrey concludes that the tangentially disposed resin cysts of *Sequoia sempervirens* represent the result of injury, and he would apply this rule to all similar cases in the various species of Abies and Tsuga.

Some years since, De Bary (9, pp. 490 and 495) formulated the law that "resin canals . . . . occur in the ligneous bundles of the same Abietineæ which possess horizontal canals in the medullary rays." This is a law of very great constancy, and, as recently shown by Penhallow (39), it is applicable without exception to all living species. But as the same author (41, p. 42) has shown more recently, *Sequoia burgessii* from the Eocene of the Northwest Territories offers a remarkable exception to this law, since it shows well defined resin passages in the medullary rays, but without corresponding structures in the vascular bundles.

As presented by existing species, Pseudotsuga, Larix, Picea and Pinus, without exception, show resin passages in both the radial and longitudinal positions. In transverse section they are scattered throughout, sometimes appearing chiefly in the summer wood, sometimes chiefly in the spring wood, or again about equally in the two regions, and they rarely conform to the precise law stated by De Bary (9, p. 495), that "they lie scattering in a ring in the external region of every annular layer." The constancy of their occurrence in the four genera mentioned involves very few features which call for special comment. In Pseudotsuga and Larix the resin passages are scattering. Sometimes they not infrequently unite in pairs so as to form short, tangential series and they thus approach the type of Tsuga or Abies, while yet again they may become definitely iso-

lated and scattering, thereby approaching the distribution of Picea and Pinus. In *Larix occidentalis* the tendency to a primitive form of distribution is expressed in the formation of a tangential zone essentially similar to that of *Tsuga mertensiana.* In both Pseudotsuga and Larix there is an obliteration of resin cells from all parts of the structure except the extreme outer face of the summer wood. In Picea, however, without exception, there is a complete obliteration of all resin cells except such as enter into the structure of the resin passages, and this is directly correlated with a higher type of structure in such passages.

In the genus Pinus, as already shown, the resin passage reaches the highest degree of organization in all respects. It shows little if any tendency to those primitive associations which are expressed in the formation of tangential series, while it has entirely replaced the isolated resin cells which are never to be found in that genus.

If, then, we ask what value such structures have for taxonomic purposes we find them to be of well defined importance. It has already appeared that in Tsuga the occurrence of resin cysts is of well defined value for specific differentiation, and the same rule is also applicable to *Sequoia sempervirens* and to four species of Abies. In the higher Abietineæ, inclusive of Pseudotsuga, Larix, Picea and Pinus, the invariable association of resin passages in the wood and in the medullary rays not only serves to separate these genera from all those in which resin cysts only may occur, but it differentiates them absolutely from all the remaining genera. Such association therefore constitutes a feature of great value. More particularly, the thin-walled epithelium of Pinus at once separates that genus from the other three, which are invariably characterized by thick-walled epithelium. Such generic differentiations are greatly emphasized by the occurrence of thyloses. These are typically developed in Pinus, where they are always thin-walled and almost invariably present. They are therefore of definite value as supplementing other features previously described. In the other genera, however, their presence in either the cyst or the resin passage, where they are generally thick-walled, is of so sporadic a nature as to give them no definite value, and we therefore find that for specific diagnoses such structures may be neglected.

Phylogenetic.

We are now in a position to present an answer to the question, "How are the resin passages related to the phylogeny of the Coniferales?" In order to present an intelligent answer to this question it will be necessary to recall the facts already discussed in connection with the resin cells and bring them into relation with our discussion of the resin passages.

In the genus Sequoia it has been shown that the general course of development of the resin cells is essentially the same as in Cupressus, etc., while it has also been shown that the genus presents in other respects a somewhat remarkable deviation. Of the two existing species, both show the distribution of the resin cells to be of the typically primitive form, *i. e.*, scattering. Nevertheless there are also in *Sequoia sempervirens* definitely organized resin cysts but without exhibiting the transitional form of a zonate disposition. Among fossil representatives Penhallow (41, p. 41) has shown precisely the same feature to be present in *S. langsdorfii*. This is the less remarkable, however, because that species is undoubtedly the ancestral form of, and practically identical with, *S. sempervirens*. The fact made clear by Jeffrey (24, p. 457), that resin cysts occur in the first annual ring of vigorous branches of adult trees, as well as in the roots of *S. gigantea*, also tends to make it apparent that the genus presents a very striking advance upon even the type presented by Juniperus, since the aggregation of resin cells and the formation of cysts from them has arisen abruptly and without the transitional forms presented by Juniperus and Taxodium. While, therefore, Sequoia is obviously related to Thuya and Cupressus on the one hand, it is on the other hand related to such types as Abies. In this sense it may be regarded as the terminal member of a developmental series embracing the Taxodiinæ, Cupressineæ, Taxoideæ as follows: —

1. Taxus and Torreya.
2. Thuyopsis.
3. Cryptomeria.
4. Podocarpus.

5. Cupressus.
6. Thuya.
7. Libocedrus.
8. Taxodium.
9. Juniperus.
10. Sequoia.

In the Abietineæ a new series is presented. This is not in any sense strictly coterminous with the first, but the two appear to make a fault, as it were, whereby there is a lateral displacement, but of such a nature that Sequoia still serves as the connecting link. Within the eleven species of Abies investigated three important phases are presented: (1) Resin cells scattering on the outer face of the summer wood, (2) resin cells grouped and forming cysts, and (3) resin cells entirely wanting. Viewing these phases in the order given, it is to be observed that in those four species which develop cysts only one shows isolated resin cells, and it is probably correct to interpret the variations noted as expressions of developmental phases in such a way that the occurrence of cysts represents the highest position. The genus Tsuga is closely related to Abies in the occurrence of isolated resin cells on the outer face of the summer wood, as also in the formation of resin cysts, but it obviously occupies an inferior position because (1) of the greater abundance of resin in the individual cells, and (2) the occurrence of definite aggregates of resin cells without the formation of cysts. This series is directly extended by those genera in which definite resin passages replace the simple cysts, since the latter are convertible into the former by easy and natural transitions. Both Pseudotsuga and Larix occupy equivalent positions because they not only present resin passages of an equal degree of development, but they show a survival of the isolated resin cells on the outer face of the summer wood. Their affinities are therefore directly with Abies and Tsuga on the lower side, but on the upper side their alliance is with Picea, which presents a very similar though somewhat higher organization of the resin passage and a complete obliteration of the isolated resin cell. Yet again, the structure of the resin passage in Picea at once connects that genus with

Pinus, in which the most complete development is attained, and it therefore terminates the series upwardly.

Having special reference to the particular forms of the secretory reservoirs, and leaving out of account all other considerations than their particular evolution, it is possible to indicate the general sequence of the genera and, to a more limited extent, of their species, as follows: —

1. Tsuga caroliniana.
   " mertensiana.
2. Abies bracteata.
   " firma.
   " nobilis.
   " concolor.
3. Sequoia.
4. Pseudotsuga and Larix.
5. Picea.
6. Pinus.

From this it is manifest that Sequoia is superior to Tsuga and Abies but inferior to Pseudotsuga, Larix, etc. But if we now view the general phylogeny with reference to the entire course of development of the resin cells and the resin passages, the relations just explained must be modified with reference to the particular position of Sequoia, and the sequence would then become: —

1. Thuyopsis and Cryptomeria.
2. Podocarpus.
3. Cupressus.
4. Thuya.
5. Libocedrus.
6. Taxodium.
7. Juniperus.
8. Sequoia.
9. Tsuga.
10. Abies.
11. Pseudotsuga and Larix.
12. Picea.
13. Pinus.

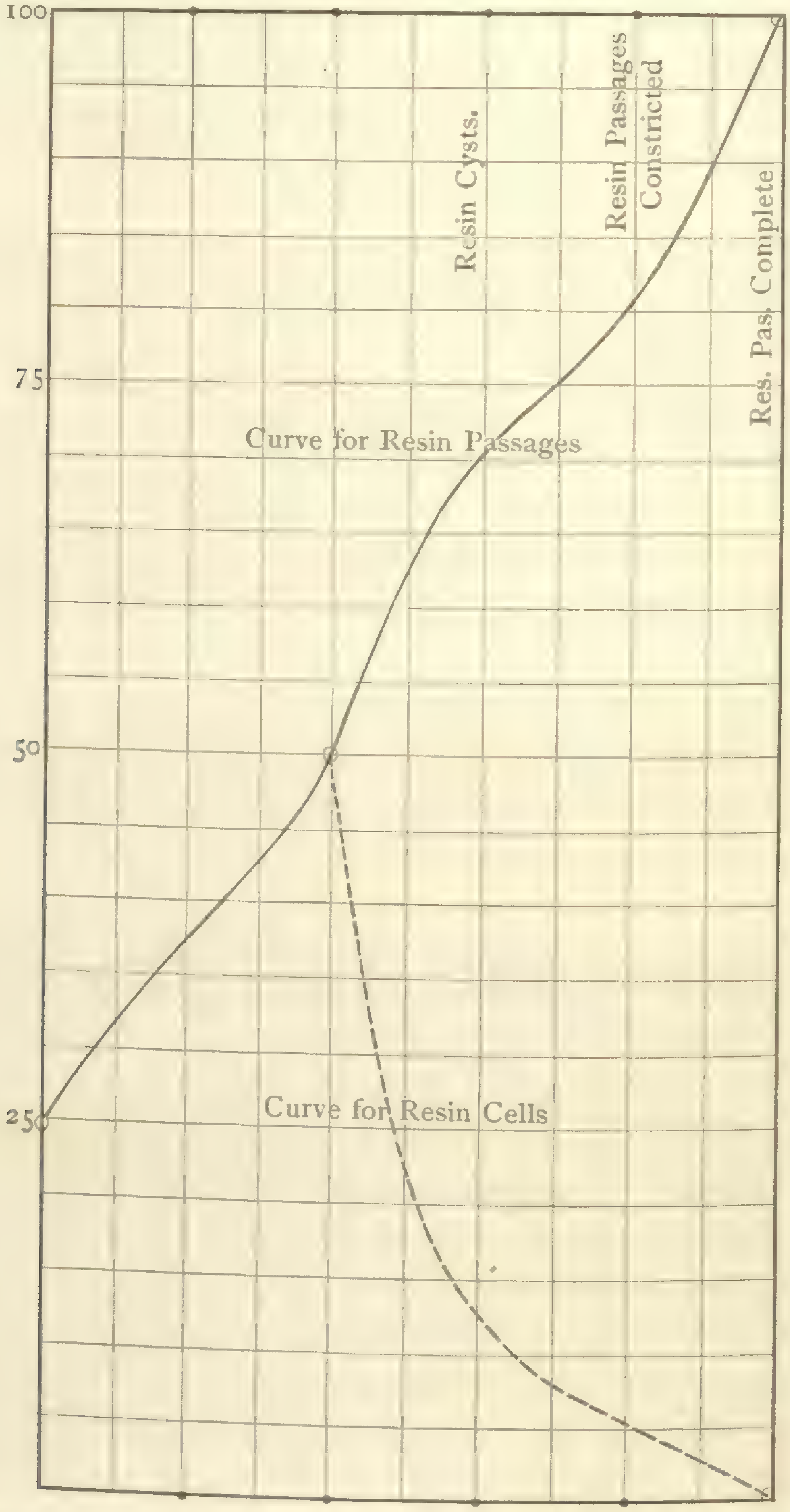
But it may assist in the general argument to view this question from another standpoint. Regarding the resin cells and the secretory reservoirs as falling within a definite series, we may apply to the various forms of distribution and to the various grades of resin reservoirs arbitrary values of such a nature as to represent our conception of their relative positions in the scale of development as expressed by percentages, thus: —

Resin cells scattering	25.0%
" " zonate	37.5 "
* " " grouped	50.0 "
" " on the outer face of the inner wood, Pseudotsuga and Larix . .	12.5 "
" " on the outer face of the summer wood, as in Abies (partial only),	5.0 "
" " wholly wanting	0.0 "
†Resin cysts, as in Tsuga, Abies and Sequoia .	70.0 "
Resin passages with constrictions, as in Pseudotsuga, Larix and Picea	80.0 "
Resin passages without constrictions and of the highest type of organization, as in Pinus .	100.0 "

We obviously have two subordinate series here, which for convenience may be regarded as coterminous, but which as already shown are "faulted" in such a way that the grouped resin cells (*) and the resin cysts (†) jointly represent the point of divergence for two separate courses of development, the latter continuing upward, while the former descends and thereby represents degradation. These features are best exhibited graphically, and the accompanying curves clearly show how, on the one hand, resin cysts and resin passages directly result from special modification of cell aggregates, while on the other hand, from the same starting point, there arises a course of degradation which finally results in the complete obliteration of the resin cell as an independent structure.

The facts thus far set forth have thrown important light upon the general course of development of certain anatomical features, and they also show the general course of development for genera

and species with reference to particular structures. They do not, however, convey any information with respect to the origin



Curve showing the approximate development of resin passages, and the corresponding obliteration of resin cells.

of the phylum as a whole, or the relations of the particular genera and species from the standpoint of collective data, and such a

discussion will be more appropriately reserved for the general summary. There is, however, one feature arising out of recent investigations which calls for consideration at this point, since certain of the conclusions reached are not in harmony with our own, the divergence of opinion indicated being the result of different methods of interpretation.

Jeffrey states (24, pp. 447 and 457) that *all* such resin cysts as occur in *Sequoia sempervirens* and Abies are of a traumatic nature, and therefore pathological. To this category he would also doubtless assign the corresponding structures of Tsuga. This opinion appears to be shared by Anderson (1 and 2), and it is also apparently supported by Pierce (42). Both Jeffrey and Anderson show that the development of such cysts is sometimes definitely associated with the production of tumors through the operation of parasites, and that they may also be induced by wounds experimentally produced. The facts they cite show conclusively that resin cysts may, and often do, arise traumatically, but in such cases they lie outside the usual course of development.

The occurrence of resin passages in the fundamental tissue of the Coniferales is a well known fact, as pointed out by De Bary (9, p. 441) many years since, when he summarized the general facts in the statement that "all investigated species of Coniferæ, with the single exception of Taxus, have resin passages or resin reservoirs which vary in distribution and number according to the species." This statement would include the leaves and bark and sometimes even the pith of species which produce neither isolated resin cells nor resin reservoirs of any kind in the xylem tissue of the stem. It directs attention somewhat forcibly to the fact that while the occurrence of resin reservoirs in the fundamental tissue is a legitimate inheritance of the mucilage canals of the Eusporangiate ferns and the Cycadofilices, as also later of the resin cells of Cordaitales, the xylem structure is the very last to receive the impress of such a course of development; and it is therefore in nowise surprising that the resin passages do not appear there until a very late period of development and that their organization can even then be brought about only through a somewhat prolonged series of changes which are initiated by the occurrence of isolated resin

cells, much as the formation of mucilage canals may be traced back to specialized cells which separately have the same function in the Eusporangiate ferns.

The local occurrence of resin passages in the xylem of the floral axis in no way invalidates the obvious conclusions to be drawn from these statements, since it may be readily accounted for in other ways. In a structure so unresponsive to influences which would induce profound alterations as the xylem, it is to be expected that important structural changes could be effected only after a prolonged interval during which the fixation of any particular character would be preceded by a period of sporadic development within which such character would be liable to recur under special conditions; and as such conditions are obviously of fundamental importance we may inquire somewhat more fully into their nature and results.

The statement of Prantl (44, p. 35) that "those genera which are devoid of resin passages in the wood of young and vigorous growth later produce single parenchyma elements in the wood, which contain resin" requires some modification in view of what Jeffrey has shown in the case of Sequoia and Abies, as well as what has been shown in the course of the present studies, and in its more comprehensive and exact form it should read, "those genera which are usually devoid of resin passages in the wood, but some species of which may nevertheless contain resin cysts in the young and vigorous growth, later produce single parenchyma elements in the wood, which contain resin."

Taken by itself this statement as applied to Sequoia and Abies might be held to indicate that the growth of the first year represents the most stable structural region of the entire stem, in the sense that it embodies characters which are most fully established, and that it will therefore embrace elements which may be eliminated from the older parts, or which may be replaced there by degenerate forms only. From this point of view it would be necessary to regard the complex resin passage as the primitive form of structure from which the cysts, groups of cells and isolated resin cells have been derived by a process of progressive degradation. This view appears to have been

adopted by Jeffrey (24, p. 454), who supports his position by citing the occurrence of resin passages in the vascular structure of the peduncle of certain fossil Cycads, interpreting this to mean that such structures represent a survival of features which have been obliterated from the structure of the stem. Such a view does not seem to be in harmony with the facts which our own studies have brought out, to the effect that resin passages of the type found in the xylem structure are in no sense primitive or vestigial, since they are wholly wanting in the primitive gymnosperms, and their organization does not arise until a very late period in the evolution of the highest forms. If our interpretation of observed facts is correct as applied to the origin of the resin passages, it shows as clearly as one could well expect a progressive development from the isolated resin cell through various phases of aggregation to the highest form of structure as found in Pinus. That there is such a series cannot be doubted and we must interpret it in one of two ways: either as progressive evolution or as progressive degeneration. To us the arguments all seem to be very emphatic with respect to lending support to the former view, most especially as all anatomical data confirm the relative positions of the genera as determined by the development of the resin passage. But assuming for the moment that the latter view is the correct one, let us see where it would lead us. It would first of all necessitate a direct reversal of the structural sequence, and this in turn would impose the necessity of placing the genus Pinus at the bottom of the scale, while those genera like Taxus, Torreya, Agathis, etc., which have no resin cells even, would be at the top. I venture to suggest that such a proposition would meet with instant opposition even from the advocates of the idea that the resin passage has preceded the other forms of resin bearing structures. The whole question appears to turn upon our recognition of what constitutes the most impressionable portions of the stem structure, and therefore the regions within which structural changes are initiated. In this connection the evidence of both palæobotany and recent botany brings out certain facts with great force and throws them into strong relief. They are as follows:

1. The mucilage canals of the Eusporangiate ferns may be regarded as the ancestral forms of the resin passages among the higher plants, but they are obviously the successors of, as they are derived from aggregates of, mucilage sacs as simple, parenchyma cells.

2. Resin passages are wholly unknown in the wood of the stem of ferns, the Cycadofilices, the Cycads, Cordaites or Araucarioxylon.

3. Resin cells are known and are abundant in the pith and bark of Cordaites, but they are absent from its wood.

4. Resin passages are known in the bark and in the pith of the Cycadaceæ, of Agathis, Araucaria and of the Coniferales in general. They also occur in the wood of the peduncles of Sequoia and Cycas, and in the xylem of the first year's growth of vigorous shoots in Sequoia and Abies. They likewise occur in the leaves generally.

5. In *Sequoia burgessii* from the Eocene, resin passages occur in the medullary rays, but they do not traverse the wood longitudinally, though isolated resin cells do occur there.

From this it would seem that the fundamental tissue is the most impressionable with respect to the development of these structures, and that after it we have in the same order the peduncle of the inflorescences and the wood of the young shoots, to which latter category would also belong the development of resin passages in fasciated stems, and such a sequence is precisely what we should expect from our knowledge of the relation which the fundamental tissue bears to other structures. According to this conception the resin passages may appear in any part of the woody structure where growth is sufficiently vigorous, but such appearance would be temporary and indicative only of a future course of development which has not as yet become sufficiently well impressed upon the organism to form a permanent feature of it. In other words, the tissue exhibits what in other cases would be termed "sports." Such structural forecasts are well known and of frequent occurrence and as applied to the development of tissues no better example is afforded than that shown by the central strand of mosses, which is generally accepted as prophetic of the future vascular system

in the sporophyte. They serve to suggest that the law of mutation as proposed by De Vries finds expression in the evolution of internal structures as well as in the development of external forms. Such cases as *Sequoia gigantea*, which shows resin cysts in the wood of the first year and nowhere else, being replaced later by resin cells, appear to us to show that young and vigorous growth in general, and therefore the growth ring of the first year, constitutes a transitional zone within which many changes of structure wholly apart from the strictly normal may arise; and such a law would similarly be applicable to the wood of peduncles. This feature is manifested in the structure of the medullary ray, the character of the tracheids as exhibited in transverse section, the genesis of the bordered pits from spiral tracheids, and in all probability also in the formation of resin passages in Sequoia and Abies as noted by Jeffrey.

Changes of this nature are to be regarded as tendencies in development in the direction of higher types of structure whereby potentialities assume a more or less definite form. From this it may be assumed that the primary growth ring is a zone within which sporadic characters are common, but it is only in the later rings that the various anatomical characters become permanently developed and properly express the normal features of structure and development.

This view is justified not only by observed facts but also by analogy which shows that as plants ascend in the scale they exhibit sporadic characters or "sports" as tendencies toward the development of otherwise potential characters. As plants gain in complexity such tendencies become manifested not simply in alterations of external form but with respect to particular details of structure and development. We therefore find ourselves compelled to conclude that the development of resin cysts and resin passages from resin cells, and the occurrence of the latter in the Coniferales, shows that all of these structures are features in the development of higher types of plants, and it is difficult for us to accept the statement of Jeffrey that such resin passages represent primitive structures and are of the nature of survivals.

Returning to the question of the traumatic nature of the

resin cysts in Sequoia, Abies and Tsuga, which Jeffrey appears disposed to formulate as a general law, it is not clear to us how this can be made to harmonize with facts coming under our own observation. It has been shown that such resin cysts occur in one species of Sequoia, four species of Abies and one species of Tsuga, yet another species of which also shows them in a potential form. The same elements appear in each case, *viz.*:—

1. The cysts assume a definite form in distribution.

2. They always occupy a definite place in the scale of structural organization.

3. They are constant features of the same species.

4. They occur at frequent intervals in the same transverse section, showing them to be repeated at intervals of from one to several years.

It is exceedingly difficult to conceive how injuries could be inflicted upon particular species with such constancy, and in such a way as to produce uniform results in the production of resin cysts which occupy a definite place in the structural scale.

It is a well known fact in the physiology of plants, that conditions which induce a premature development of parts also bring about the conversion of potentialities into actualities, and under such circumstances the latter become evidences of a pathological condition. The swamp maple normally develops a brilliant foliage in the autumn, but it is not uncommon to find individual branches which have been injured, or even entire trees, which exhibit the characteristic autumnal foliage in midsummer, a condition which is correctly interpreted as pathological. Special conditions of nutrition, *e.g.*, an excess of mineral food elements, may similarly induce a premature development of the reproductive process. It has been shown by Richards that in cases of injury the rate of respiration is greatly increased, an alteration in functional activity which he rightly interprets as due to efforts directed toward the repair of injured parts. But this implies a local increase of nutritive materials and their application to a more intensive process of nutrition. Such features are well known in the case of all hypertrophies, and they must be similarly applicable to all forms of wounds, no matter what their origin, differing only in degree. We cannot

very well conceive of such profound functional disturbances without assuming a corresponding alteration in or development of those structures upon which the activities are dependent. The structural alterations may thus become characteristic, *local* features, and they may even represent the tangible expression of potentialities which are not manifested elsewhere in similar regions of the plant body. Furthermore, normal resin canals are invariable features of Larix, Pseudotsuga, Picea and Pinus. But Anderson (1, p. 29, etc.) has shown that in *Picea excelsa*, *Larix japonica* and *Pinus strobus* there is an enormous increase in the number of resin canals, arising through the unusual stimulus afforded by the operations of the mycelium of *Agaricus melleus*. With respect to *Abies firma* he also clearly shows that the general effect of the stimulus afforded by the parasite *Æcidium elatinum* (which gives rise to hexenbesen) is to produce a more perfectly organized form of the secretory reservoir than is present under normal conditions. To us, therefore, these facts offer a reasonable explanation of the appearance of resin cysts under conditions of injury, when they assume a pathological rôle, while they also serve to harmonize their occurrence under such circumstances with the general course of their evolution as already set forth.[1]

The results to which we are now brought are based entirely upon developmental phases in anatomical elements of the vascular cylinder. While our studies lead us to certain definite conclusions, we do not in any sense regard the latter as final, but only as affording one step in the solution of a question which must be viewed not only from the broader standpoint of more extended anatomical data, but from that of Physiology as well, although we feel disposed to insist that the final answer will be found to rest chiefly upon an anatomical basis. That there may be room for a different interpretation of the facts here recorded, is quite possible, since Dr. Jeffrey has recently permitted me to

[1] Since the above was written, Dr. Jeffrey has very kindly shown me several specimens which appear to afford strong evidence in support of his position, and in view of such facts the conclusions here stated are made with reserve until further evidence is at hand through the publication by him of studies now in progress.

examine the manuscript of an important contribution to our knowledge of the Abeitineæ, in which he brings out very significant facts suggestive of the idea that this group is of a much more primitive character than has hitherto been supposed, or than is indicated by our own studies. It is therefore of importance that final judgment should be suspended until the results of these various studies, as well as those of Coulter and Chamberlain, all directed to the same end but prosecuted along entirely distinct lines, can be brought together and co-ordinated. It is in this sense, therefore, that we offer the following.

Summary and General Conclusions.

In discussing the phylogeny of the higher Gymnosperms, three subordinate phyla must be taken into consideration in the following order:—(1) Cordaitales, (2) Ginkgoales, (3) Coniferales.

Regarding the Cordaitales as the most primitive gymnospermous stock of which we have present knowledge, it is possible to trace its origin to the Cycadofilices. The genera Lyginodendron, Heterangium, Calamopitys and Pityoxylon present many structural features which are common to all, and which not only establish their relation to the Cycadean line of descent, but they offer many suggestions of that course of development which is realized in the higher Coniferales. They therefore constitute the real starting point for two lines of descent, the first of which embraces the Cycadales. With this we have little or nothing to do at the present moment, beyond establishing its probable relation to the other gymnosperms. The second line emerges in a type of plants having characteristics distinctly allied to those of the Coniferæ, and it is this line of descent with which we are now chiefly concerned. It is now possible to define the origin of this phylum somewhat more exactly than Coulter has done (7 & 8), since there is good reason to believe that it emerges from the Cycadofilices through Poroxylon. Scott (52, p. 398) has already pointed out the relations of this genus to the Cycadofilices and the Cycadaceæ on the one hand, and to Cordaites on the other, so clearly as to remove the necessity for detailed

discussion at this time, beyond giving emphasis to one or two important structural relations. It has been noted that in *Calamopitys saturni*, the most primitive distribution of the bordered pits upon both the radial and tangential walls, is represented in the protoxylem structure. Such distribution, however, undergoes rapid modification whereby it is wholly limited to the radial walls in the secondary wood. A similar limitation appears in other, somewhat closely related genera, and it is fully expressed in Poroxylon where the multiseriate disposition and hexagonal form are typically preserved, though there is, at the same time, a tendency to segregation to such an extent that the pits sometimes become round. In this it is possible to notice the first indication of a character which, while infrequent, is nevertheless occasionally expressed among the Cordaitales, though it is generally characteristic of the related phyla Ginkgoales and Coniferales.

Among the Cordaitales there is but one genus (Cordaites) which we have heretofore been accustomed to associate with that phylum, and, so far as our present knowledge goes, it undoubtedly stands in the closest relations to Poroxylon. It is, however, improbable that the two were in any sense coterminous, and it is altogether probable that there may have been some one or more intermediate forms of which we have no present knowledge. Our present studies on the other hand, show clearly, that we must bring into this phylum two other genera of an obviously higher degree of development, but which have commonly been ranked with the Abietineæ and which, according to Eichler (11), occupy the highest position in the scale. This position is untenable upon anatomical grounds which give us reason to believe that Agathis and Araucaria (including, of course, Araucarioxylon) are not only inferior to the Coniferales as a whole, but that they are distinctly Cordaitean. Accepting this view, and the fact that Agathis is the inferior genus, the sequence would place Cordaites at the base and Araucaria at the top, with Walchia as the immediately ancestral form of the latter. This relation is not only natural, but it is justified on anatomical grounds.

The tendency to segregation of the bordered pits as exhibited by Poroxylon suggests the relation of this genus to others in

which such a feature is fully expressed, and it thereby forms the basal member of another series. From the opposite point of view, it has been shown that the occurrence of two-seriate pits in Pinus and others of the Coniferales, as well as in Ginkgo, points to a common origin for such genera in a type with multiseriate, hexagonal pits, and that both Agathis and Araucaria must likewise center in the same generalized form. This gradual convergence is justified on other grounds, and the genus Poroxylon among known forms most nearly fulfills the requirements of the case. We may therefore look upon it as lying between the Cycadofilices and all the higher gymnosperms, giving rise to two lines of descent, the first of which embraces the Cordaitales as already described, while the second shortly divides once more. This secondary division gives rise on the one side to the Ginkgoales, and on the other to the Coniferales. The anatomical data already discussed when viewed collectively show that the general sequence within the latter would be (1) the Taxoideæ, (2) the Taxodiinæ, (3) the Cupressineæ, (4) Abies, (5) Tsuga, (6) Pseudotsuga, (7) Larix, (8) Picea and (9) Pinus, of which one division (II) represents the highest type of development. The sequence of species for each genus cannot always be determined with a full measure of satisfaction, and these difficulties may possibly be made clear by reference to a particular case. The succession of the two species of Sequoia is difficult to determine on purely anatomical grounds, but the general tendency of the facts already recited is to give to *S. sempervirens* the more primitive position, a view which is sustained by its palæontological history.

The relations brought out in the foregoing studies, and the conclusions reached, may be made more obvious without the tedious method of a detailed discussion by reference to the accompanying table of anatomical data, which substantially summarizes all the results derived from the study of particular structures.

Data for Table of Anatomical Characters, in identical series.

1. Spiral tracheids.
2. Bordered pits in 1–3 rows.
3. Bordered pits in 1–2 rows.
4. Bordered pits in one row.
5. Pits on the tangential walls of the summer wood.
6. Lateral walls of the ray cells with bordered pits.
7. Uniseriate rays.
8. Terminal walls of the ray cells thin and entire.
9. Resin cells.
10. Terminal walls of the ray cells locally thickened.
11. Terminal walls of the ray cells strongly pitted.
12. Ray tracheids.
13. Resin passages.
14. Fusiform rays.
15. Thyloses in the resin passages.
16. Lateral walls of the ray cells with simple pits.
17. Ray cells of two kinds.

1. Resin cells scattering.
2. Resin cells zonate.
3. Resin cells grouped.
4. Resin cells on the outer face of the summer wood.
5. Ray tracheids marginal.
6. Ray tracheids interspersed.
7. Ray tracheids dentate.

A. Number of species.
B. Percentage value of genus.

TABLE OF ANATOMICAL CHARACTERS OF THE CORDAITALES, GINKGOALES AND CONIFERALES.

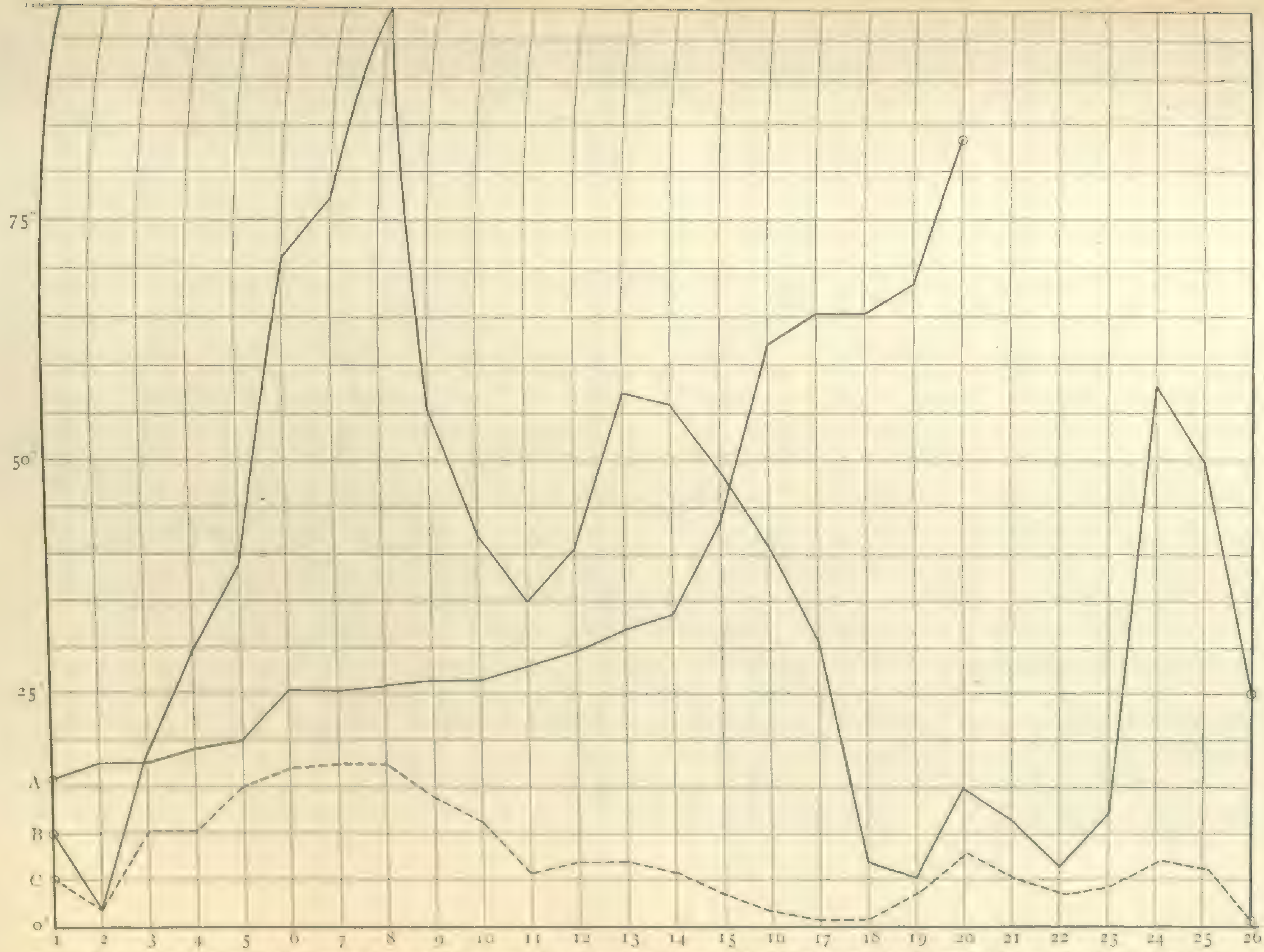
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
1 Agathis australis.	—	×			×	×	×	×																	1	16.
2 Araucaria cunninghami.	—	×			—	×	×	×																	3	17.7
excelsa.	—	—	×		—	×	×	×																		
bidwillii.	—	—	—	×	—	×	×	×																		
3 Ginkgo biloba.	—	—	×		×	×	×	×																	1	17.7
4 Torreya taxifolia.	×	—	×		—	×	×	×																	3	19.0
californica.	×	—	—	×+	×	×	×	×																		
nucifera.	×	—	—	×	—	×	×	×																		
5 Taxus floridana.	×	—	—	×—	×	×	×	×																	4	19.9
canadensis.	×	—	—	×	×	×	×	×																		
brevifolia.	×	—	—	×	×	×	×	×																		
cuspidata.	×	—	—	×	×	×	×	×																		
6 Thujopsis dolabrata.	—	—	—	×	×	×	×	×	×									×							1	25.4
7 Cryptomeria japonica.	—	—	—	×	×	×	×—	×	×									×							1	25.4
8 Podocarpus macrophylla.	—	—	—	×	×	×	×	×	×									×	(o)						1	25.9
9 Taxodium distichum.	—	—	(1)	×	×	×	×	×	×									(1)	×						1	26.4
10 Libocedrus decurrens.	—	—	—	×+	×	×	×	×	×	(o)								(1)	×						1	26.4
11 Thuya gigantea.	—	—	—	×+	×	×	×	×	×										×						3	28.2
occidentalis.	—	—	—	×+	×	×	×	×	×									×	(o)							
japonica.	—	—	—	×+	×	×	×	×	×			×						×				×				
12 Sequoia sempervirens.	—	—	×		×	×	×	×	×				×—		×			×		×					2	29.7
gigantea.	—	—	×		×	×	×	×	×									×								
13 Cupressus lawsoniana.	—	—	(1)	×	×	×	×	×	×									×	×						9	32.0
pisifera.	—	—	—	×+	×	×	×	×	×										×							
obtusa.	—	—	—	×	×	×	×	×	×									×	×							
macrocarpa.	—	—	—	×+	×	×	×	—	×	×								×	(o)							
arizonica.	—	—	—	×	×	×	×	—	×	×								×		×						
macnabiana.	—	—	—	×	×	×	×	—	×	×									×							

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
13 Cupressus goveniana.	—	—	—	×	×	×	×	—	×	×								×								
thyoides.	—	—	(1)	×	×	×	×	—	×	×		×						×	(o)			×				
nootkatensis.	—	—	—	×	×	×	×	—	×	×		×						×	×			×				
14 Juniperus virginiana.	—	—	—	×+	×	×	×	—	×	×								—	×						11	33.4
nana.	—	—	—	×	×	×	×	—	×	×		(1)						—	×							
rigida.	—	—	—	×	×	×	×	—	×	×								—	×							
californica.	—	—	—	×	×	×	×	—	×	×	(o)							—	×							
utahensis.	—	—	—	×	×	×	×	—	×	×	(o)							—	×							
sabinoides.	—	—	—	×	×	×	×	—	×	×	(o)							—	×							
communis.	—	—	—	×	×	×	×	—	×	×	(o)							—	×							
sabina.	—	—	—	×	×	×	×	—	×	×	(o)							—	×							
pachyphloea.	—	—	—	×	×	×	×	—	×	—	×							(1)	×							
monosperma.	—	—	—	×	×	×	×	—	×	—	×								×							
occidentalis.	—	—	—	×	×	×	×	—	×	—	×								×							
15 Abies fraseri	—	—	—	×+	×	×	×	—	—	—	×							—	—						11	43.5
lasiocarpa.	—	—	—	×	×	×	×	(1)	—	—	×							—	—							
veitchi.	—	—	—	×	×	×	×	—	—	—	×							—	—							
balsamea.	—	—	(1)	×	×	×	×	—	—	—	×	×						—	—	—	×	×				
magnifica.	—	—	—	×	×	×	×	—	×	(1)	×							—	—	—	×					
amabilis.	—	—	—	×+	×	×	×	—	×	—	×							—	—	—	×	×				
grandis.	—	—	—	×	×	×	×	—	×	(1)	×							—	—		×	×	×			
bracteata.	—	—	(1)	×	×	×	×	×	×	—	×		×—					—	—	×						
nobilis.	—	—	—	×+	×	×	×	—	×	—	×		×—					—	—	×						
concolor.	—	—	—	×	×	×	×	—	×	×	(1)		×—		×			—	—	×	×					
firma.	—	—	(1)	×	×	×	×	—	×	—	×		×—					—	—	×						
16 Tsuga canadensis.	—	—	×		×	×	×	—	×	—	×—	×						—	—	—	×	×	×		5	62.2
sieboldii.	—	—	—	×+	×	×	×	—	×	—	×	×						—	—	—	×	×	×			
caroliniana.	—	—	—	×	×	×	×	—	×	—	×	×						—	—	×	×	×				
pattoniana.	—	—	—	×	×	×	×	—	×	—	×	×						—	—	—	×	×	(o)			
mertensiana.	—	—	—	×	×	×	×	—	×	—	×	×	×—					—	—	×	×	×				

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
17 Pseudotsuga douglasii.	×	—	—	×+		×	×	—	×	—	×	×	×	×				—	—	—	×	×	(o)		2	65.2
macrocarpa.	×	—	—	×	×	×	×	—	×	×		×	×	×				—	—	—	×	×	(o)			
18 Larix occidentalis.	—	—	×		×	×	×	—	×	—	×	×	×	×				—	—	—	×	×			4	65.2
americana.	(1)	—	×		×—	×	×	—	×	—	×	×	×	×				—	—	—	×	×	(o)			
lyallii.	—	—	—	×+	×	×	×	—	×	—	×	×	×	×				—	—	—	×	×	(o)			
leptolepis.	—	—	—	×	×—	×	×	—	×	—	×	×	×	×				—	—	—	×	×	(o)			
19 Picea breweriana.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×			10	68.5
rubra.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×	(o)			
alba.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×	(o)			
engelmanni.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×				
jesoensis.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	(1)			—	—	—	—	×	(o)			
polita.	—	—	—	×+	×	×	×	—	—	×	—	×	×	×	(1)			—	—	—	—	×	(o)			
bicolor.	—	—	—	×	×—	×	×	—	—	(1)	×	×	×	×	(1)			—	—	—	—	×	×			
pungens.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	(1)			—	—	—	—	×	(o)			
nigra.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	×			—	—	—	—	×	(o)			
sitchensis.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	×			—	—	—	—	×	(o)			
20 Pinus. Sec. I.																										
parryana.	—	—	—	×	×	×	×	—	—	×	(1)	×	×	×	×			—	—	—	—	×	(o)		41	83.3
cembroides.	—	—	—	×	×	×	×	—	—	(1)	×	×	×	×	×			—	—	—	—	×	(o)			
monophylla.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	×			—	—	—	—	×	×			
balfouriana.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	×			—	—	—	—	×	(o)			
aristata.	—	—	—	×	×	×	×	(1)	—	—	×	×	×	×	×		×	—	—	—	—	×	(o)			
edulis.	—	—	—	×	×	×	×	(1)	—	—	×	×	×	×	×		×	—	—	—	—	×	(o)			
lambertiana.	—	—	×		×	—	×	×	—	(1)	—	×	×	×	×	×		—	—	—	—	×	(o)			
monticola.	—	—	—	×+	×	—	×	×	—	(1)	—	×	×	×	×	×		—	—	—	—	×	×			
flexilis.	—	—	—	×	×	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)			
reflexa.	—	—	—	×	×	—	×	×	—	(1)	—	×	×	×	×	×		—	—	—	—	×	(o)			
strobus.	—	—	—	×	×	—	×	×	—	(1)	—	×	×	×	×	×		—	—	—	—	×	(o)			
parviflora.	—	—	—	×	×	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)			
albicaulis.	—	—	—	×	×	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)			

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
20 Pinus. Sec. II.																										
clausa.	—	—	×		—	×	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
rigida.	—	—	—	×+	—	×	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
serotina.	—	—	(1)	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
banksiana.	—	—	(1)	×	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
contorta.	—	—	—	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
glabra.	—	—	—	×	—	—	×	×	—	—	—	×	×	×	×	×	(1)	—	—	—	—	×	×	×		
echinata.	—	—	—	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
resinosa.	—	—	—	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
koraiensis.	—	—	—	×+	—	(1)	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
thunbergii.	—	—	—	×	—	(1)	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×		×		
densiflora.	—	—	—	×	—	(1)	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
murrayana.	—	—	—	×+	—	(1)	×	×	—	×	—	×	×	×	×	×		—	—	—	—	×	×	×		
arizonica.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
coulteri.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×		×		
tuberculata.	—	—	—	×+	—	(1)	×	×	—	×		×	×	×	×	×	×	—	—	—	—	×	×	×		
torreyana.	—	—	—	×+	—	—	×	×	—	×		×	×	×	×	×	×	—	—	—	—	×	(o)	×		
chihuahuana.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
jeffreyi.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
ponderosa.	—	—	—	×	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
scopulorum.	—	—	—	×	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
pungens.	—	—	—	×+	—	×	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
inops.	—	—	—	×+	—	(1)	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
muricata.	—	—	—	×+	—	—	×	×	—	—	×	×	×	×	×	×	×	—	—	—	—	×	×	×		
insignis.	—	—	—	×+	—	—	×	×	—	—	×	×	×	×	×	×	×	—	—	—	—	×	×	×		
sabiniana.	—	—	×		—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	(o)	×		
tæda.	(1)	—	×		—	—	×	×	—	—	—	×	×	×	×	×	(1)	—	—	—	—	×	×	×		
palustris.	—	—	×		—	—	×	×	—	—	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
cubensis.	—	—	×		—	—	×	×	—	×	×	×	×	×	×	×	×	—	—	—	—	×	×	×		

In preparing this table, the various anatomical features have been chosen with reference to (1) the constancy of their occurrence, (2) their structural prominence and (3) their obvious relation to diagnostic purposes. In their horizontal extension, an attempt has been made to arrange them in accordance with the law of frequency, as well as with reference to their relation to development, in such wise that while the spiral tracheid is assumed to be the most primitive type of the vascular structure, the presence of two kinds of cells in the medullary ray may be held to express the highest form of development. To the members of the series so constituted we may then assign arbitrary values in arithmetical sequence from one to seventeen; while those subordinate characters which are represented by different forms of distribution may be regarded as forming a second series similarly valued. Any primitive or other character which has become obliterated through development may be held to retain its original value with respect to the general course of such development, and it is always indicated by —. Vestigial structures occurring sporadically are designated by (1), and to them one half the value of the fully developed character is assigned. All normal features are designated by ×, which becomes × + when they show development toward the next higher form, or by × — when they show a definite tendency to degeneration. Sporadic characters which are obviously in the line of development are indicated by (0), but they are assigned only half values. On this basis it is possible to arrange a sequence of genera and species in such a manner as to exhibit a progressive development from the simple Agathis with a minimum of characteristics to the complex Pinus in which the greatest number of anatomical features are involved. Furthermore, through such a series it is possible to determine the relative position of the various genera by percentage values, and this gives the most valuable insight into the approximate relations of the various members within the general line of descent. Such relations are determined not only for each anatomical character, but for the collective characters. Reducing these facts to a graphic form, the accompanying curves will assist in making the relations more clear, especially in emphasizing the general course of develop-



Curves for sequence of genera and frequency of anatomical characters, of the Cordaitales, Ginkgoales and Coniferales. A = Sequence of genera. B = Specific characters. C = Generic characters.

ment which in its final form is best expressed by a biological tree. A figure of this sort is difficult to construct, and there is no agreement among investigators as to the particular form it should take. While the figures in common use indicate a certain relationship in descent, they completely fail to convey any impression of the way in which the succession arises, and they furnish no indication of possible gaps. They therefore constitute a very poor working basis.

I have long been accustomed in teaching to compare the various lines of descent among plants with the branchings of a deliquescent tree, since it has always seemed reasonable to suppose that the laws which govern the branching of a limb, which give rise to all the varying forms of arrested development, and which thereby determine a particular modification of the figure which would otherwise result from unmodified growth, must be equally applicable to the general evolution of the higher forms of plants from a common ancestral type. In endeavoring to secure a natural growth which would best express all the conditions involved, a sympodium was first of all suggested, inasmuch as it conveys the idea of succession through lateral members in such a way as to indicate the direct line of descent. But sympodia as we usually know them fail to adequately express the idea of arrested development and suppression in their various forms. In the branching of *Acer platanoides* all the conditions appear to be met in a very satisfactory manner. The branch of the Norway maple, when of vigorous growth, is a monopodium, and it is obvious that such would not answer the object in view, since its most prominent feature would suggest the idea of a continuous series of coterminous members from which lateral members would arise at intervals. There is no evidence that any phylum represents such a series; on the contrary there is every reason to believe that such relations do not exist among the various groups of plants.

But in those branches of the Norway maple which exhibit slow growth various forms of arrested development are manifested. These take the form of atrophied buds, or of branches in all stages of development, and there thus arises a modified monopodium which eventually becomes, in many cases at least,

Diagrammatic representation of the Phylogeny of the Coniferales.

a true sympodium. In comparing this with the monopodial branch of vigorous growth, it appears that the alterations involve more than mere suppression. In the monopodium the average angle of divergence for the lateral members is 45.3°, while for the derived form it is 34.1°. The latter will be seen to completely fulfill all conditions with respect to the development of a phylum, even to indicating the position of missing members. Selecting from this such portion as may serve the requirements of the present case, we obtain the following figure which may be held to embody our final conclusions as to the general succession of the different gymnosperms, and from it we may gather that the highest representative — Pinus — is the terminal member in the main line of descent from the Cycadofilices through Poroxylon, while from such a central line both the Cordaitales and Ginkgoales have been given off as side lines. In the construction of this figure an attempt has been made to show all normally developed buds (o) and their relative dimensions; atrophied buds (o), the position of which is recognizable; and atrophied branches (/ –) which are still visible, but it is obvious that the figure does not show many members, all evidence of the former existence of which has completely disappeared.

The general results of these investigations serve to confirm in a very striking manner the probable monophyletic origin of the Gymnosperms as already expressed by Coulter (7), while they also show that the real transition ground, at least for all but the Cycadaceæ, was probably represented by Poroxylon as indicated by Scott (52).

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STUDIES ON THE PLANT CELL.—IV.

BRADLEY MOORE DAVIS.

SECTION III. HIGHLY SPECIALIZED PLANT CELLS AND THEIR PECULIARITIES (*Continued*).

4. The Spore Mother-cell.

THE spore mother-cell and its homologues the pollen mother-cell and certain embryo-sacs have furnished some of the most interesting subjects for cell studies in the plant kingdom. Sporogenesis in all plants above the thallophytes seems to be a period when nuclear structures are especially clearly differentiated and when the mechanism of mitosis reaches the highest degree of complexity. These intricate conditions are only equalled by processes in the development of the female gametophyte of some angiosperms, and during endosperm formation, also in the events of spermatogenesis and with the segmentation of the egg nucleus of certain gymnosperms.

Sporogenesis is one of the critical periods in the life history of a higher plant since it is the time when the asexual generation (sporophyte) passes over to the sexual (gametophyte). This provides certain important features such as the reduction phenomena concerned with chromosomes and greatly adds to the interest in these cells. These matters will receive special attention in Section V, but they must be borne in mind to appreciate fully the significance of many events of spore formation.

The general history of the spore mother-cell may be described as follows: It is the product of the last mitosis in the reproductive tissue called the archesporium. This mitosis always presents the number of chromosomes characteristic of the sporophyte which is double the number found in the gametophyte. Therefore the nucleus that passes into the spore mother-cell has the sporophyte number of chromosomes. Two

mitoses occur successively in the spore mother-cell in all forms. The first mitosis presents half the number of chromosomes found in the last nuclear division in the archesporium and is consequently the reduced or gametophyte number. The reduction of the chromosomes then takes place during the period of rest between the last mitosis in the archesporium and the first in the spore mother-cell. There are two mitoses in the spore mother-cell. In some forms these are exactly alike and present essentially the same characters as the usual typical mitoses of plants. But among the spermatophytes there are likely to be peculiarities in the arrangement and distribution of the chromosomes. In consequence the first mitosis may be heterotypic and the second homotypic in contrast to the normal typical conditions. The description and explanation of these characters will be reserved for the groups that illustrate them the best. They have nothing to do with qualitative reduction phenomena as was formerly supposed.

There is sometimes a well defined period of rest after the first mitosis with the formation of a wall between the two daughter nuclei, but frequently the second mitosis follows immediately after the first so that the spore mother-cell comes to contain four daughter nuclei. Cell walls may then be formed between these nuclei simultaneously so that the resultant spores are disposed in a radially symmetrical arrangement that is termed tripartite. These cell divisions are almost universally present in the spore mother-cell, the only exceptions being certain spermatophytes whose megaspore mother-cells develop directly into embryo sacs, the two mitoses (heterotypic and homotypic) being included within these structures and forming a part of the gametophyte history. Why the number of spores should generally be four is unexplained. There does not seem to be any physiological significance in the number or other reasons why it should not be more or less. Indeed it is somewhat variable in the spermatophytes for microspore or pollen mother-cells form two and three pollen grains in certain types and five, six and seven have been found in others, while much larger numbers have been occasionally reported. In no case is the microspore mother-cell known to develop directly into a pollen grain, al-

though the megaspore mother-cell regularly becomes an embryo sac in some forms (*e. g.*, Lilium). But an increasing number of observations indicate that the megaspore mother-cell generally develops two, three or four potential megaspores although normally only one of these becomes an embryo sac.

The interest in the protoplasmic activities of sporogenesis lie chiefly in the elaborate methods of spindle formation and mechanism of mitosis, in the organization and distribution of the chromosomes, in the functions and activities of the nucleolus, and in the organization of the cell plate and development of the cell wall. There is a very extensive literature on the spore mother-cell some of which, however, merely treats the broad features noted in studies of a general morphological character on the development of sporophylls or floral structures. We shall only attempt to consider the most important contributions, and for convenience will begin our treatment with the Hepaticæ and conclude with the spermatophytes where the conditions are the most complex.

The Hepaticæ or liverworts furnish some remarkable spore mother-cells, and are now the subject of considerable interest and some discussion. They were first brought conspicuously to the attention of botanists by a paper of Farmer ('94) on *Pallavicinia decipiens*. Farmer described a remarkable series of events in this type. The nucleus of the spore mother-cell became surrounded before division by dense protoplasm that extended into the four lobes of the cell in the form of a four-rayed star which he called a "quadripolar spindle." After its development four chromatic droplets appeared in the nucleus to indicate its approaching division. These chromatic droplets became four chromosomes which by division were doubled in number. The eight rod shaped chromosomes moved in pairs towards the four lobes of the spore mother-cell. There was a further division of each chromosome, making sixteen in all, and the four groups of four each passed simultaneously to the poles of the "quadripolar spindle" which persisted to the end. It should be noted that the striking peculiarities of Farmer's account lie in the division of the four primary chromosomes into sixteen, and in their simultaneous distribution through a "quadripolar

spindle" to form at once four daughter nuclei. These events are unparalleled, as far as the writer is aware, in the plant or animal kingdom, and consequently the account deserves especial attention. A four-rayed figure around the nucleus is not surprising because the spore mother-cell of the Jungermanniales is four lobed, and its centrally placed nucleus lies in a restricted area. But the simultaneous distribution of quadrupled chromosomes to form four daughter nuclei is a process whose establishment would be of fundamental significance. Farmer also described a centrosome at each pole of the "quadripolar spindle."

Farmer ('95*a*, *b*, and *c*) followed his paper on Pallavicinia with studies on other liverworts. He reported the "quadripolar spindle" in the early stages of mitosis in several of the Jungermanniales, but did not find the quadrupling and simultaneous distribution of the chromosomes as in Pallavicinia. The "quadripolar spindle" when present was a temporary structure replaced later by the bipolar spindles of two successive mitoses with a longer or shorter interval between. Farmer considers the "quadripolar spindle" of these forms as transitional between that of Pallavicinia and the normal bipolar spindle. The Ricciales, Marchantiales and Anthocerotales present two successive mitoses after the usual manner in the spore mother-cell.

The writer has described the events of sporogenesis in Pellia (one of the Jungermanniales) in a paper covering the nuclear activities at several periods in its life history (Davis, :01), and confirmed much of Farmer's account of the mitoses in this spore mother-cell. These are two in number and successive, with a very well defined resting period between the first and the second. There is a four-rayed figure present during the prophase of the first mitosis, and this seems to correspond to Farmer's "quadripolar spindle." The nucleus lying in the center of the four lobed spore mother-cell becomes invested by a kinoplasmic sheath which develops a fibrillar structure. Many of these fibrillae extend into the lobes of the spore mother-cell because the nucleus is confined to a narrow space in the constricted central region of the cell and the lobes offer the only possible relief for the crowded conditions. However, the four-rayed structure is not present when the chromosomes are ready for distribution,

but there is found instead one large, broad poled spindle. (See Fig. 5 *c*.) A cell wall is formed between the two daughter nuclei (Fig. 8 *d*) which divide again after a very short period of rest, the two spindles lying at right angles to one another. The poles of the spindles are rather blunt, and there are no centrosomes or centrospheres in either mitosis. The four-rayed structure of prophase must be regarded as preliminary to spindle formation because the chromosomes are not ready for distribution, and when that period arrives the structure has been replaced by the true spindle of the first mitosis. These facts led me to question Farmer's account of mitotic phenomena in Pallavicinia and his conception of the "quadripolar spindle," and I suggested that this structure might prove to be a phenomenon of prophase, a view to which Farmer (:01) has taken exception in a criticism of my results.

Recent investigations of Moore (:03) on Pallavicinia are flatly contradictory to the conclusions of Farmer for *Pallavicinia decipiens* and support my suggestions. Moore finds that there are two mitoses in the spore mother cell of *Pallavicinia lyellii*, the second (Fig. 12 *c*, *d*) following immediately upon the first (Fig. 12 *b*), each with bipolar spindles and without centrosomes. The chromosomes, eight in number, appear in the usual way with each mitosis (Fig. 12 *c*, *d*). There is no "quadripolar spindle" in Farmer's sense, no quadrupling and simultaneous distribution of the chromosomes. The prophases preceding the first mitosis present a tetrahedral form as is shown in Fig. 12 *a*. This is accentuated by the fibrillae which gather at the points to make a four-rayed structure extending into the lobes of the spore mother-cell. This condition is identical with similar stages in Pellia and in other leafy liverworts, and is a feature to be expected from the fact that the spindle fibers develop chiefly or wholly externally to the nuclear membrane in a rather crowded region of the cell. The nucleus at this time is unquestionably in prophase as shown by the undifferentiated chromosomes and because this stage passes immediately into a bipolar spindle of the normal type (Fig. 12 *b*). It seems very probable that Farmer was mistaken in his conclusions for *Pallavicinia decipiens*, and that the mitoses in the spore mother-cell of this form

are not different in any essentials from those of other plants.

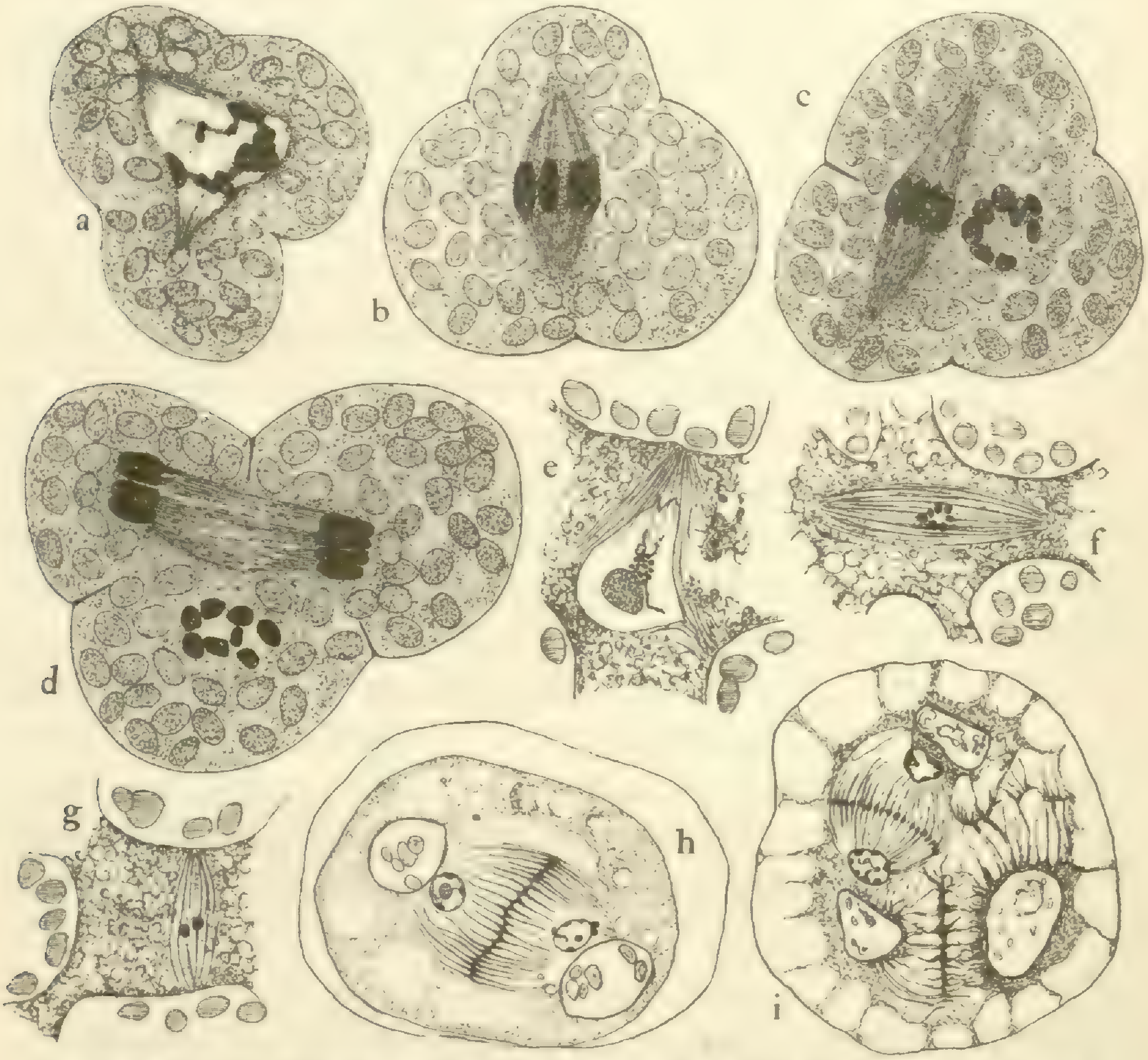

FIG. 12.—Spore mother-cells of Hepaticæ. *a, b, c, d, Pallavicinia lyellii.* *a*, Prophase; the fibrillæ gathered on four sides of the nucleus which has a tetrahedral form pointing into the four lobes of the spore mother-cell; the nuclear membrane has not yet broken down; similar stages of prophase were probably considered by Farmer as quadripolar spindles. *b*, metaphase of the first mitosis; the spindle in all respects a normal bipolar structure without centrospheres. *c*, Metaphase of the second mitosis: one spindle shown in side view, the other, almost perpendicular to the first, presents the eight chromosomes at the nuclear plate. *d*, anaphase of the second mitosis: one spindle viewed from the side, the other from one end shows the group of eight grand-daughter chromosomes. *e, f, g, anthoceros laevis*. *h, i*, a larger species from Italy. *e*, prophase: one pole of spindle developed. *f*, just after metaphase of the first mitosis; eight chromosomes; blunt poled spindle without centrospheres. *g*, metaphase of second mitosis; very small spindle. *h*, cell plate forming in the spindle between two nuclei. *i*, two nuclei at the side of their respective chromatophores and the cell plate between, after the second mitosis; a third chromatophore shown with strands of protoplasm connecting it with other regions of the cell. (*a, b, c, d*, after Moore, :03; *h, i*, after Van Hook, :00.)

The "quadripolar spindle" proves to be nothing more than a condition of prophase.

Besides Pellia and Pallavicinia, which are the most thoroughly studied of the lower liverworts, we know the processes of sporo-

genesis in the highest type, Anthoceros (Davis, '99). This form is exceedingly attractive for such investigations because the spore mother-cells may be found in all conditions upon the same sporophyte. However, the small size of the nuclei and spindles is a disadvantage. Just previous to the first mitosis the nucleus becomes surrounded by a mesh of delicate fibrillæ (kinoplasmic). Later the nucleus takes an angular form, and the fibrillæ are found conspicuously at the prominent poles (Fig. 12 *e*). The nuclear membrane breaks down and the fibers become arranged to form a bipolar spindle (Fig. 12 *f*) without centrosomes or centrospheres. There is a short period of rest after the first mitosis, but no wall is formed between the two daughter nuclei. The small spindles of the second mitosis (Fig. 12 *g*) are likewise bipolar. They lie at right angles to one another and the cell plates that are laid down determine, in part, the position of the walls that are formed between the four granddaughter nuclei and which divide the spore in a tripartite manner. These cell plates are very small (Fig. 12 *h* and *i*), but they have been observed in a favorable species of Anthoceros by Van Hook (:00). It is not clear how these plates become extended to the wall of the spore mother-cell unless (as suggested in Sec. II) their edges make use of planes of vacuoles when the protoplasm separates to develop the cleft between the four daughter cells. The poles of the spindles in Anthoceros are flattened and entirely free from structures that might be considered centrosomes.

Other interesting events of sporogenesis in Anthoceros are the division of the chromatophores and the nuclear condition termed synapsis. The young spore mother-cell contains a single large chromatophore. This increases greatly in size and becomes filled with starch grains. The chromatophore divides successively into two and then four portions which arrange themselves symmetrically in the cell with the nucleus in the center. The mitoses then follow and the four daughter nuclei are distributed, one for each chromatophore in the cell. This provision of four chromatophores long before the mitoses in the cell seems very remarkable (Davis, '99, p. 94 and 95). Synapsis is a condition very common in the nucleus of spore mother-cells before division. The chromatic material becomes gathered into a compact

mass besides the nucleolus. The significance of synapsis is not clear, but the subject will be discussed in Section VI. However, there is good evidence from Anthoceros that the phenomenon is a normal event and not an artefact, because synapsis is always found at a certain period of sporogenesis, and nuclei in neighboring spore mother-cells a little older or younger present their chromatic material with the usual arrangement (Davis, '99, p. 96 and 97).

To summarize the conditions in the spore mother-cells of the Hepaticæ, all conclusions, in the author's opinion, indicate: (1) That the spindles develop from a surrounding weft of fibrillæ without the assistance of centrosomes. (2) That the mitoses are always two in number and successive with the same number of chromosomes for each division. (3) That the cell walls may be formed successively as in Pellia and some other of the Jungermanniales or simultaneously, to give tetrahedral spores, as in Anthoceros, types of the Marchantiales and Ricciales, Pallavicinia and some companion forms in the Jungermanniales. It will be interesting to note the essential agreement in these matters between the Hepaticæ and the higher plants.

Nothing is known of the nuclear activities during sporogenesis in the other great division of the bryophytes, the mosses (Musci). The spore mother-cells in this group are always small and unattractive for cell studies but the Sphagnales appear to be rather the most promising for such investigations, which are greatly to be desired.

The pteridophytes have furnished some important contributions to our knowledge of the spore mother-cell. There is first the paper of Osterhout ('97) on spindle formation in Equisetum, which was one of a group of three contributions (Mottier, '97, Juel, '97) that did much to dispose of a then prevalent belief that the development of the spindle in higher plants was controlled by centrosomes. This investigation was followed by a study of Smith (:00) on spindle formation in Osmunda. Calkins ('97) and W. C. Stevens ('98*a*) considered especially the formation and reduction of chromosomes in several of the ferns, and arrived at contradictory conclusions. Strasburger (:00, p. 76 to 79) has reviewed these results in relation to studies of his own on Osmunda.

Osterhout's ('97) account of spindle formation in Equisetum is noteworthy. He found that the nucleus of the spore mother-cell became surrounded by a web of delicate fibrillæ, which, extending radially into the surrounding cytoplasm (Fig. 13 *a*), were later (Fig. 13 *b*) gathered into numerous pointed bundles or cones. After the dissolution of the nuclear membrane these

FIG. 13.—Spore mother-cells of Pteridophytes. *a, b, c, Equisetum limosum.* *a*, prophase of first mitosis; the radially disposed fibrillæ are gathering together into cones. *b*, prophase, older than *a*; the nuclear membrane has broken down and the fibrillæ have entered the nuclear cavity; the cones lie in two groups opposite one another. *c*, just before metaphase; the fibrillar cones are nearer together and the chromosomes have gathered to form the nuclear plate. *d, e, f, g, Osmunda regalis.* *d*, very early prophase of the first mitosis; nucleus in the spireme stage surrounded by a granular and fibrillar zone of kinoplasm. *e*, prophase, somewhat older than *d*; fibrillar kinoplasm showing polarity. *f*, still older; chromosomes formed; one pole of spindle developed. *g*, metaphase; a tri-polar spindle. (*a, b, c*, after Osterhout, '97; *d, e, f, g*, Smith, :00.)

cones arranged themselves side by side in two sets to form the spindle of metaphase (Fig. 13 *c*). The spindle is then from the outset multipolar, and even though some of the cones unite when they become grouped around a common axis, nevertheless the poles of the spindle at metaphase show their composite nature in the absence of a common focal point for the fibrillæ. There are no centrosomes at the poles and no reason for their presence at any stage in the process of spindle formation.

Smith's (:00) study of Osmunda presents an important confirmation of Osterhout's conclusions that the spindle in pterido-

phytes developed without centrosomes, while illustrating a process of spindle formation along somewhat different lines. Smith distinguished a zone of kinoplasm around the nucleus previous to spindle formation. This zone became granular, and then the granules arranged themselves in rows to form fibrillæ (Fig. 13 *d*), which, however, did not extend into the cytoplasm radially, but lay generally parallel to one another, so that the spindle appeared bipolar from the beginning (Fig. 13 *e*). One pole of the spindle was generally formed considerably in advance of the other (Fig. 13 *f*). The fibers did not meet at a common point but over a broad area, and there were no centrosomes. There is, then, normally no multipolar stage in Osmunda, although tripolar spindles (Fig. 13 *g*) were occasionally found. During anaphase secondary fibers were put forth from the vicinity of the daughter nuclei and these met in the equatorial region of the cell. The spindle of the second mitosis was formed exactly as in the first. After this division the four granddaughter nuclei lay connected with one another by six spindles (two primary and four secondary). Cell plates were laid down in the equatorial regions of these spindles so that the protoplasm became divided simultaneously and symmetrically into tetrahedral spores.

The studies of Calkins ('97) and Stevens ('98*a*) were chiefly upon the division and distribution of the chromosomes in connection with reduction phenomena. Calkins believed that the processes of sporogenesis followed the same course as the maturation of sexual cells in animals, with a transverse division to give a qualitative reduction in Weismann's sense. Stevens disagreed with Calkins in several particulars, holding that the reduction was merely quantitative. Reduction phenomena in plants is now much better understood than at the time of these papers which dealt with plants much more difficult to study than some other forms (*e. g.*, types of the Liliaceæ). We shall consider the subject in Section V, but may state now that Calkins' conclusions have not been sustained.

Strasburger (:00) gives considerable attention to spindle formation in his well known review and critique of cytological literature. He proposes the following classification of spindles in higher plants which lack centrosomes. Those that pass

through multipolar stages and later become bipolar are called multipolar polyarch spindles. When the spindle has a well defined axis from the beginning, as is generally true of the cells in vegetative tissues of higher plants, it is termed multipolar diarch. Strasburger has shown that these types, while easily separated in the extremes, grade into one another so that the classification is not founded on distinctions of a very fundamental character. The spindle of Osmunda, for example, resembles a multipolar diarch, but its method of development is more closely related to that of other spindles in spore mother-cells (multipolar polyarchs) than to those of vegetative tissues.

The gymnosperms offer in Larix an excellent subject for studies on the formation of pollen, and this type has been treated in several important papers, notably by Belajeff ('94*b*), Strasburger ('95) and Allen (:03). Belajeff's contribution is important as the first investigation that considered the multipolar spindle as a preliminary stage in the development of the bipolar structure. Other authors, at this time and previous to his publication, had noted multipolar and tripolar spindles (Strasburger ('80) and ('88) in several forms), but the lily had received the greatest attention in this connection (Farmer ('93) and ('95*d*), Strasburger ('95), Sargent ('97) and Mottier ('97)). Mottier's investigation presented the first detailed account of spindle formation in this angiosperm and will be discussed presently.

Allen's (:03) paper on Larix includes one of the best discussions of the literature bearing on the subject of spindle formation that has yet appeared. He finds that the cytoplasm around the nucleus just previous to mitosis comes to contain a loose network of fibrillæ. Some of the fibers may be followed through the nuclear membrane and may be seen attached to chromatin bodies in the interior (Fig. 14 *a*). Later the cytoplasmic fibrillæ become arranged radially and extend from the nucleus even to the outer plasma membrane at the periphery of the pollen mother-cell. The radiating fibers are connected with one another by branches which indicate that the structure is in part an expanded condition of the original network, but the fibers also grow. The fibers now fold over so that they tend to lie parallel to

the surface of the nucleus and thus form a dense felt around the nuclear membrane. Presently the nuclear membrane which was before a definite film becomes wavy in outline and often granular in appearance. The nucleolus shows signs of dissolution and there is a marked increase in the number of intranuclear fibers, which are chiefly or wholly of nuclear origin. After the

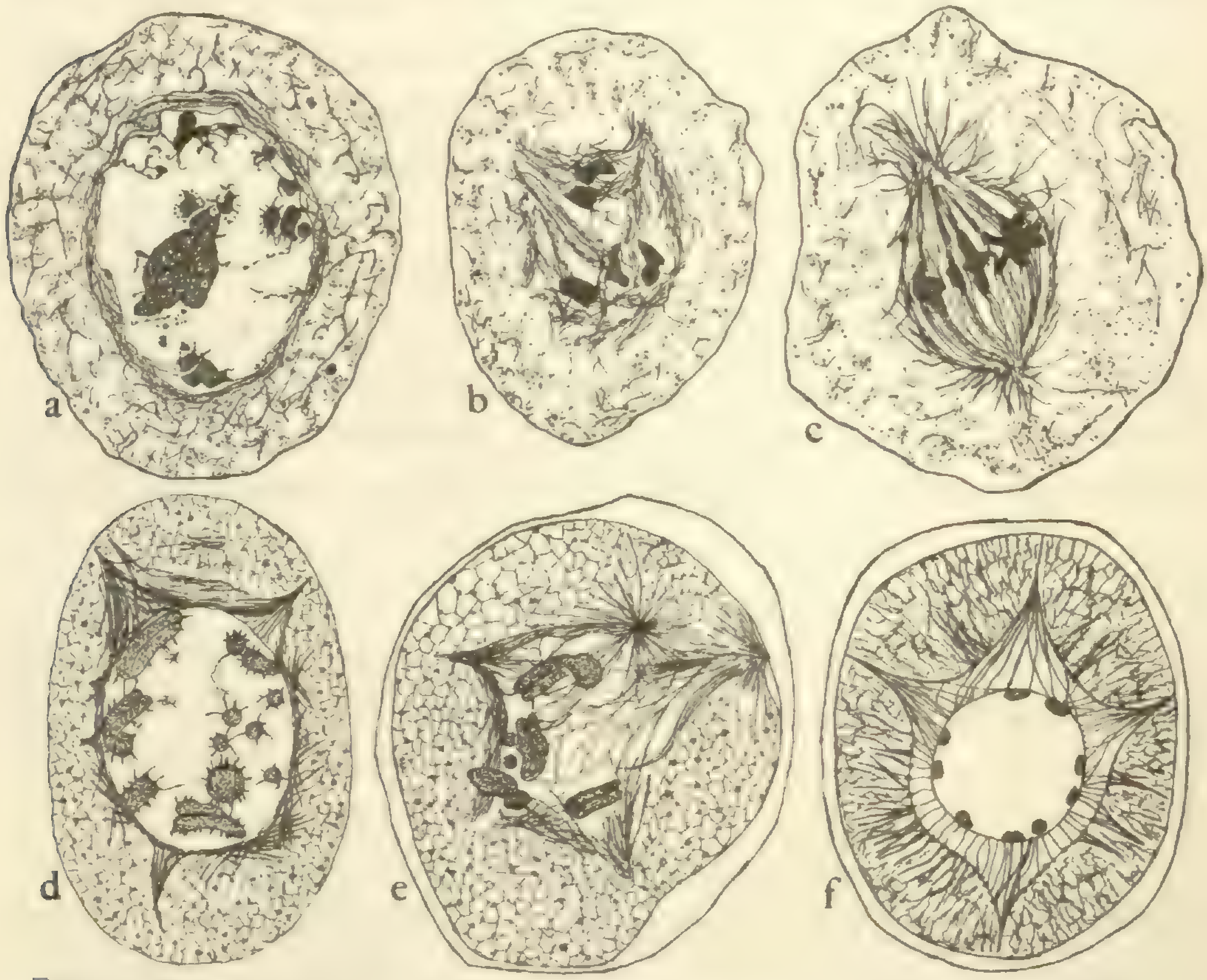

Fig. 14.—Pollen or microspore mother-cells of spermatophytes. *a, b, c, Larix europea. a,* prophase of first mitosis; kinoplasmic fibrillæ forming a felt around the nucleus. *b,* late prophase; the nuclear membrane has broken down and the interior space has become filled with fibrillæ which have gathered to form a multipolar spindle. *c,* metaphase; a completed spindle with polar radiations. *d, e, Lilium candidum. d,* prophase of first mitosis; the kinoplasmic fibrillæ have formed a net around the nucleus and are gathered into several cones which would have become poles of the spindle. *e,* late prophase; the nuclear membrane has disappeared and the fibrillæ are entering the nuclear cavity; several cones of the fibrillæ constitute the multipolar spindle. *f, Agave Americana.* Prophase of the first mitosis; the spindle cones on the upper side have pushed through the special membrane around the nucleus. (*a, b, c,* after Allen, :03; *d, e,* Mottier, '97; *f,* Osterhout, :02.)

disappearance of the nuclear membrane some of the peripheral fibers push outward to form several cones of a multipolar figure (Fig. 14 *b*). The fibers attached to the chromosomes gather into bundles that extend towards these poles. Finally the bundles of fibers become more regular and straighten out so that they come to lie approximately parallel to one another, and thus

the multipolar structure, developing a distinct axis (Fig. 14 *c*), becomes bipolar (multipolar polyarch). There is no central body at the poles and no place for a centrosome in this developmental history.

The first detailed study of spindle formation in Angiosperms was, as before stated, that of Mottier ('97) which treated especially of Lilium, Podophyllum and Helleborus. This paper with one by Juel ('97) on Hemerocallis and Osterhout ('97) on Equisetum effectually disposed of previous views very generally held (Guignard, '91, followed by other authors), that spindle formation and mitotic phenomena in higher plants was involved with the activities of centrosomes or other kinoplasmic centers. Mottier found that the nucleus in the pollen mother-cell of the lily became invested just before mitosis with radiating fibers that shortly after increased in quantity to form a felted web around the structure. Some of the fibers gathered into cones (Fig. 14 *d*) which pointed towards the periphery of the cell so that there resulted, with the disappearance of the nuclear membrane and the entrance of the fibers into the nuclear cavity, a multipolar spindle (Fig. 14 *e*). The poles gradually came to lie parallel to one another in a common axis, some of them disappearing, so that the spindle generally became distinctly bipolar at metaphase (multipolar polyarch). Essentially the same history was repeated during the second mitosis in the lily.

From this time on there have been a succession of papers verifying the general conclusions of Mottier and Juel and extending these results to many other forms until now it seems to be well established that centrosomes are never present in the pollen mother-cell and that multipolar spindles, developed from felted stages and changing to bipolar spindles, may be expected in most if not all forms. Guignard ('97 and '98) described multipolar spindles in several types (Nymphæa, Nuphar, Limodendron, etc.), and while he believed that these poles were occupied by granules that sometimes fused to form typical centrosomes, nevertheless he admitted that the multipolar spindle might be formed independently of centrosomes.

The most important papers on spindle formation in Angiosperms following those of Mottier ('97 and '98) and Juel ('97)

have been Lawson ('98) on Cobea, W. C. Stevens ('98*b*) on Asclepias, Atkinson ('99) on Arisæma and Trillium, Duggar ('99) on Bignonia, Wiegand ('99) on Convallaria and Potamogeton, Gregoire ('99) on Lilium and Fritillaria, Guignard ('99) on Naias, Williams ('99) on Passiflora, Duggar (:00) on Symplocarpus and Peltandra, Lawson (:00) on Gladiolus, Byxbee (:00) on Lavatera, Andrews (:01) on Magnolia and Liriodendron, Schniewind-Thies (:01) on Galtonia and Osterhout (:02) on Agave.

Of the papers listed above several demand especial attention for the completeness of the studies on the early stages of spindle formation in the pollen mother-cell. Lawson ('98 and :00) found that the nuclei of Cobea and Gladiolus previous to mitosis were surrounded by a zone of granular kinoplasm which he named perikaryoplasm. This zone developed a felted envelope of fibrillæ from which projections extended to form the cones of a multipolar figure. The cones by fusing in two groups developed the bipolar spindles. The spindle fibers of Gladiolus are formed entirely from the perikaryoplasm, the nucleolus and linin apparently taking no part in the development of the spindle. The nucleolus remains intact until after the dissolution of the nuclear membrane when the spindle is practically completely organized. Miss Williams ('99) found for Passiflora that the nuclear cavity became filled with a network developed from the linin. The nuclear wall became also transformed into a mesh which connected the network from the linin with the surrounding cytoplasmic reticulum, thus forming a continuous system throughout the cell. The central region of this network, enclosed by a granular zone, developed a multipolar figure whose poles finally fused to form a bipolar spindle. The contrast between this type of spindle in which so much of the fibrous structure is derived from the linin and that of Gladiolus just described is very marked. A granular region outside of the fibrous network around the nucleus is much more conspicuous in Lavatera, described by Byxbee (:00), than in Passiflora. It forms in Lavatera a dense zone that suggests a gathering of nutritive material (deutoplasm). The fibrillæ are developed as a felt around the nuclear membrane and enter the nuclear cavity

with the breaking down of this structure. The fibers gather into projecting cones presenting a multipolar structure, and two of these, becoming more prominent, absorb the others and thus form a bipolar spindle.

One of the most recent studies on spindle formation is that of Osterhout (:02) on Agave. This investigation is of especial interest for the extensive experimentation in the technique of fixation. The author proposes a new terminology for the stages of mitosis that need not be presented here. Agave offers a striking peculiarity in the presence of a special membrane around the early stages of the spindle. The fibrillæ form inside of this membrane and finally push through it radially into the exterior cytoplasm where they gather into cones (Fig. 14 *f*). The cones separate into two opposite groups with a general parallel arrangement of the fibers and in this manner a bipolar spindle is formed.

It is becoming possible to make some general statements respecting the methods of spindle formation in the spore mother-cell. Just previous to prophase it is almost always possible to differentiate a region of kinoplasm around the nucleus. This zone has been found to be either granular, *e. g.*, Pellia, Anthoceros (Davis, '99 and :01), Osmunda (Smith, :00), Cobea and Gladiolus (Lawson, '98 and :00), or it presents the appearance of a fibrous reticulum, *e. g.*, Equisetum (Osterhout, '97), Larix (Allen, :03), Lilium (Mottier, '97 and '98), etc. The latter condition probably develops from the former by the arrangement of granules into fibers and the gradual expansion of a very close network thus formed into a coarser structure. The fibers in this reticulum sometimes surround the nucleus as with a heavy web. They later extend radially into the cytoplasm, partly by the expansion of the network and partly by their own growth and frequently take a radial arrangement. In some instances the spindle fibers are developed very largely within the nucleus from the linin (Passiflora, Williams, '99). They then become gathered into bundles or groups forming the cones which collectively constitute a multipolar figure that is often called a multipolar spindle. By the rearrangement of these cones somewhat parallel to one another, together with more or

less fusion, the multipolar structure becomes a bipolar spindle (multipolar polyarch) generally just previous to the period of metaphase. The formation of cell plates and the disappearance of the spindle fibers have been discussed in Section II under the title "Cleavage by cell plates."

Mention should be made of some irregularities in the division and distribution of the chromosomes that are conspicuous in certain spore mother-cells and which have been the cause of much discussion. The subject has especial reference to certain older views of the reduction phenomena in plants. Chromosomes split once longitudinally in all typical mitoses and the halves are drawn apart in a symmetrical manner which is very easily understood. This division is really determined by the longitudinal fission of the spirem thread. But appearances during the first nuclear division in the spore mother-cell of many forms have puzzled investigators for many years and have given rise to a number of interpretations. It seems to be pretty clearly established now that in these types there is a double longitudinal splitting of the chromosomes at the time of this mitosis. The first division takes place during prophase and the second follows closely after the first and is generally clearly seen at metaphase or during anaphase. Therefore the chromatic bodies which appear at the nuclear plate during the first mitosis are in reality divided or about to be divided into quarters and they separate after this mitosis as pairs of granddaughter chromosomes instead of simple daughter elements. These pairs are either firmly united at one end into a V or irregularly drawn out so that the bodies have very unusual and sometimes bizarre forms. Nuclear figures of this irregular appearance were originally described by Flemming for the first mitosis in the spermatocyte of Salamandra and named by him "heterotypic." These in the spore mother-cell of plants are of similar character and the designation "heterotypic" has been adopted by botanists for this condition. The pairs of chromosomes that enter the daughter nuclei after the first mitosis fuse end to end to form a spirem thread which breaks up again during the second mitosis, without longitudinal fission, into pairs of chromosomes which are believed to be identical with those that entered the nucleus after the first mitosis. Since there is

no longitudinal splitting of the spirem thread before the second division this mitosis differs from that of the "typical" mitoses of cells and is called "homotypic" to distinguish it on the one hand from the former and on the other from "heterotypic" divisions. Several illustrations of heterotypic and homotypic mitoses to be described presently are presented in Fig. 15, showing the peculiar V-shaped pairs of granddaughter chromosomes, characteristic of the first group. It is important to note that whatever the significance of this premature fission of the chromosomes before the second mitosis it is not of the nature of a qualitative reduction division in Weisman's sense. The details and significance of reduction phenomena will be considered in other connections (Section V). The topics discussed above have been recently studied and reviewed by Mottier (:03).

We have as yet said nothing of the megaspore mother-cell in Spermatophytes. An increasing number of investigations have clearly established the fact that the embryo-sac in many forms is one of a group of two, three or four cells, each of which is a potential megaspore because its nucleus contains the reduced number of chromosomes. We are accustomed to think of the well known conditions in the lily, where the megaspore mother-cell develops directly into the embryo-sac. But this type with some others (*e. g.*, Fritillaria, Tulipa, Erythronium, etc.) are the exceptions and present a very highly differentiated condition in which the usual developmental history is shortened in a very interesting manner, which will be described presently.

The embryo-sac arose undoubtedly as one of four megaspores developed after essentially the same manner as microspores or pollen grains, excepting that their arrangement was generally in a row, which is even true of some pollen grains (*e. g.*, Asclepias, Zostera). As stated above, an increasing number of investigations have established the row of four potential megaspores in a large number of forms in various groups. They may not always be distinguished by the form of the group, but their homologies are established by the mitoses that lead to their differentiation. Two mitoses are of course required to establish the group of four cells and both are identified by the reduced number of chromosomes. Some detailed studies on these mitoses have

established the fact for certain forms that the first is heterotypic and the second homotypic, exactly as in divisions of the micro-

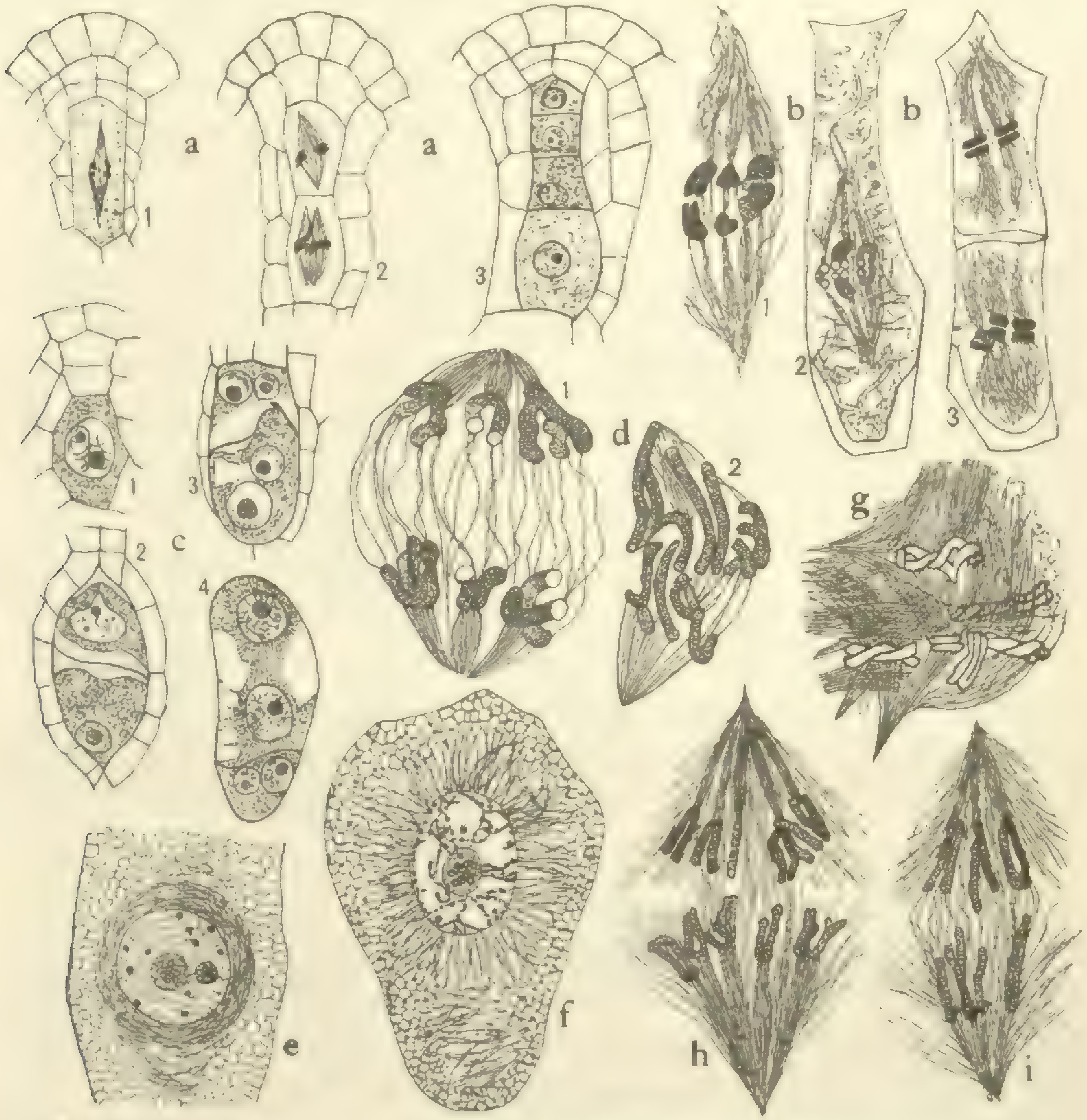

FIG. 15.— Embryo sac or megaspore mother-cell of spermatophytes. *a*, *b*, *Galtonia candicans*. *a*1, first mitosis in megaspore mother-cell. *a*2, second mitosis. *a*3, group of four megaspores. *b*1 and *b*2, shortly after metaphase of the first mitosis (heterotypic). *b*3, metaphase of the second mitosis (homotypic). *c*, *d*, *Scilla Sibirica*. *c*1, megaspore mother-cell. *c*2, after the first mitosis. *c*3, after the second mitosis, the lower cell of the pair to become the embryo sac. *c*4, after the second mitosis, the upper cell of the pair to become the embryo sac. *d*1, anaphase of the first mitosis (heterotypic). *d*2, anaphase of the second mitosis (homotypic). *e*, *Lilium martagon*: portion of embryo sac mother-cell, nucleus surrounded by a felt of fibrillæ. *f*, *Lilium candidum*; embryo sac mother-cell, nucleus surrounded by radiating fibrillæ. *g*, *h*, *i*, *Lilium martagon*. *g*, late prophase of first mitosis in embryo sac mother-cell, a multipolar spindle. *h*, anaphase of first mitosis (heterotypic). *i*, anaphase of second mitosis (homotypic). (*a*, *b*, *c*, *d*, after Schniewind-Thies :01; *e*, *f*, *g*, *h*, *i*, Mottier '97.)

spore or pollen mother-cells. Schniewind-Thies (:01) figures very completely the mitoses in Galtonia. The first mitosis in the megaspore mother-cell (Fig. 15*a*) is heterotypic because the

chromosomes (Fig. 15*b*, 1, 2) show clearly the V-shaped forms characteristic of this division. The second mitosis (Fig. 15 *b*, 3) is homotypic. The lowest cell of the group of four (Fig. 15 *a*, 3) becomes the embryo-sac and the mitoses that take place within it as the female gametophyte develops are all typical. This account illustrates a simple history in megaspore mother-cell development and is considered the first of three types in a classification proposed by Schniewind-Thies (:01).

The second type of development is one in which two megaspores are generally developed from a mother-cell and one of these becomes the functional embryo-sac. Schniewind-Thies presents an excellent illustration of this type in Scilla. The first mitosis in the megaspore mother-cell (Fig. 15 *c*) is heterotypic (Fig. 15 *d*, 1) and results in two cells (Fig. 15 *e*). The second mitosis in both cells is homotypic (Fig. 15 *d*, 2). Either the lower (Fig. 15 *e*, 3) or the upper (Fig. 15 *e*, 4) of the pair may become the embryo-sac. The embryo-sac then includes the homotypic or second mitosis within its development, making it the first nuclear division of the gametophyte history. The typical mitoses of the gametophyte begin with the second nuclear division in the embryo-sac. Three megaspores may be formed in such a group when the cell of the pair that does not become the embryo-sac divides again.

The third type of development is illustrated by several forms, of which the best known are Lilium (Mottier, '98 and :03) and Tulipa (Schniewind-Thies : 01). The lily has been much studied, but Mottier presents the most detailed account of spindle formation and the behavior of the chromosomes. He supports the observations of Schniewind-Thies, based upon the tulip, and her explanation of this type of development. The megaspore mother-cell of the lily and tulip develops directly into the embryo-sac. The first mitosis in this cell (Fig. 15 *h*) is heterotypic and the second (Fig. 15 *i*) homotypic. These divisions give the four-nucleate embryo-sac and one more mitosis presents the mature structure. This last is a typical mitosis, the only one found in the embryo-sac before the development of the endosperm and sporophyte embryo. Thus the two mitoses characteristic of the spore mother-cell are here included within the

embryo-sac and appropriated as a part of the gametophyte history.

We can see in these three types of embryo-sac development an evolutionary process of which the third stage is plainly derived from the simpler second and first, and is consequently a highly developed and very complex condition, far removed from primitive gametophyte structures among the angiosperms. The embryo-sacs of these forms (Lilium, Tulipa, Fritillaria, Erythronium, etc.) are probably the most complex spore mother-cells that we know The studies of Schniewind-Thies and Mottier have been supported by other investigations, and more especially by the results of Ernst (:02) on *Paris quadrifolia* and *Trillium grandiflorum*, who followed the history of the heterotypic and homotypic mitoses in these forms in detail. They illustrate the second type of embryo-sac development in the classification of Schniewind-Thies.

Spindle formation in the embryo-sac mother-cell has not received as much attention as in the pollen mother-cell, probably because material of the latter structures may be obtained much more readily than the former. There have been numerous descriptions and figures of the spindles but few accounts in full of their development. Of the latter the investigation of Mottier ('98) on Lilium is the most complete. This paper was written at the time when the centrosome question was under discussion and served, with other papers on the spore mother-cell (Osterhont, '97, Juel, '97, Mottier, '97) to discredit the presence of these bodies in this structure. Mottier found that the nucleus of the embryo-sac became invested with a close network of fibrillæ (Fig. 15 *e*) from which fibers developed into the cytoplasm radiating from the nucleus in all directions (Fig. 15 *f*). With the dissolution of the nuclear membrane the fibrillæ entered the nuclear cavity, filling it with masses of fibers which gathered into cones to form a complicated multipolar spindle (Fig. 15 *g*). These cones later come together into two poles, but even in the mature spindle the fibrillæ are frequently in several groups at the poles. Essentially the same history is repeated in the second mitosis. A large number of later papers have described and figured multipolar spindles in embryo-sacs, con-

firming the conclusions of Mottier that these structures are developed here after the same methods as in the pollen mother-cell, from surrounding investments of fibrillæ and without centrosomes. Indeed the embryo-sac is remarkable for the quantity of the cytoplasmic fibrillæ present during its mitoses.

In concluding this account attention should be called to some forms whose microspore mother-cells were formerly supposed to omit the mitoses of sporogenesis and develop directly into pollen grains. These conditions were reported in Zostera, the Cyperaceæ, and the Asclepiadaceæ. However, Juel (:00) finds the two mitoses present in *Carex acuta*, although three of the nuclei break down and the cytoplasm is appropriated for the fourth to form a single pollen grain whose wall is developed from that of the mother cell The history is very similar to the development of the megaspore in certain heterosporous pteridophytes (*e.g.*, Marsilia, Selaginella) and to the embryo-sac, which functions while its companion potential megaspores degenerate. The development of the pollen in the Asclepiadaceæ has been shown to be normal in the nuclear activities by several investigators (Frye, :01, Strasburger, :01, and Gagner, :02), the tetrad consisting of four pollen grains in a row, instead of the usual arrangement. In Zostera (Rosenberg, :01) there are longitudinal divisions of the very much elongated pollen mother-cell to give four extraordinary filiform pollen grains.

5. The Cœnocyte.

This remarkable type of cell has reached an extraordinarily high state of development in certain plants, notably among the Siphonales and the filamentous Phycomycetes (Mucorales, Saprolegniales and Peronosporales). Cœnocytes are multinucleate cells. The simplest types are developed by the limited division or fragmentation of a nucleus accompanied by an increase in the size of the cell but without extended growth. Excellent illustrations are found in the older cells of the red algæ, the internodal cells of the Characeæ and in old parenchyma cells of many higher plants.

A higher type of cœnocyte is presented when the multinucle-

ate cells show some definite activity resulting in extensive growth or peculiarity of form. Thus some laticiferous cœnocytes are branching tubes that grow for considerable distances among the cells of the tissues in which they are contained. The embryo-sac and the female gametophytes of Selaginella and Isœtes in the early stages of their development are interesting cœnocytes. Among the lower algæ there are numbers of cœnocytic forms (*e. g.*, Hydrodictyon, Cladophora) whose cells present very little change with age except an increase in size. Yet some of these conditions, especially those illustrated in the Cladophoraceæ, are probably related to the higher types of cœnocytes.

The best differentiated cœnocytes are found in the Siphonales, Mucorales, Saprolegniales and to a lesser extent among the Peronosporales and are especially well illustrated in a few aquatic forms, such as Monoblepharis and Myrioblepharis. The peculiarities of these forms lie in elaborate structures which result from the ability of the cœnocyte to respond to several directive stimuli in its growth. The most complicated responses and consequently the most highly differentiated morphology is shown among the Siphonales, where some very elaborate forms are found. In many types the plant body is clearly composed of root and shoot regions and in the highest expressions (*e. g.*, some species of Caulerpa) there are rhizoids, shoots and leaf-like structures presenting a remarkable degree of specialization. The behavior of the protoplasm in these most highly differentiated types of the Siphonales is known to us chiefly through studies of Noll and Klemm.

There is a very conspicuous layer of clear protoplasm next to the cell wall which constitutes an outer plasma membrane (hautschicht). This outer plasma membrane is stationary while the granular protoplasm within changes its position readily and frequently in different portions of the plant streaming in various directions. The nuclei are all situated in the granular cytoplasm so that they must shift their positions with its movements. Noll ('87) by a clever method of coloring the cell wall of living plants of Caulerpa was able to prove that the forward growth took place by the protoplasm extending beyond the old wall, thus adding new regions of cellulose to the old. He called this

method of growth a process of eruption in contrast to Nägeli's conception of growth by intussusception. Increase in thickness comes with the laying down of successive lamellæ inside the older wall and is consequently growth by apposition. Caulerpa is very favorable for such investigations and Noll's results greatly strengthen the theory that a cellulose wall results from the direct transformation of a plasma membrane in which carbohydrate molecules gradually replace those of albuminous material. Accordingly the cellulose wall is not strictly a secretion and its growth is not by the intercalation of new molecules among the old (intussusception) in a non-living membrane.

The wide space in the interior of the filaments of Caulerpa and some other members of the Siphonales is frequently crossed by cellulose bars at various angles. These are at first strands of protoplasm which become gradually filled with a carbohydrate material and finally solidified. Noll ('88*a*), while recognizing that these structures may have value in strengthening the filament, believes that they are also the paths of metabolic exchange between the interior regions of the protoplasm and the water outside the plant. They are surrounded by the plasma membrane which in consequence presents a much greater extent of surface to the water permeating the cell wall.

It is plain that because of the constant movement of the granular cytoplasm carrying with it the nuclei which change their position in the cell, the outer plasma membrane is the only portion of the protoplasm that can receive fixed stimuli for an extended period. Consequently Noll regards this membrane as the responsive or irritable region of the cell that reacts to the stimuli which largely or wholly direct growth. Some of these stimuli are well established. Thus it is light which directs the formation of leaves and shoots. The behavior of Caulerpa in relation to prominent stimuli (light, darkness, gravity, etc.) has been studied by Noll ('88*b*) and Klemm ('93). The latter author believes that the response is due to the presence of foods or other substances at certain points which make them especially sensitive to the external stimuli. Injuries to a filament of the Siphonales brings about an immediate flow of protoplasm to the wounded part (Klemm,' 94), after which the plasma membrane is quickly repaired and new portions of the wall laid down.

Mitotic phenomena in the Siphonales is known to us only through the investigations of Fairchild ('94) on Valonia. He found that nuclei in the same individual may divide directly or indirectly. The first process is one of simple fission, the latter takes place with the formation of an intranuclear spindle. Studies in sporogenesis and gametogenesis are very much to be desired in the Siphonales that we may understand the behavior of the nuclei at these periods. The author's recent studies of oögenesis in Vaucheria (Davis, :04*a*) have shown an interesting process of nuclear degeneration similar to that in the Saprolegniales and Peronosporales, and suggests some very interesting lines of investigation.

The protoplasmic structure in the hyphæ of the larger filamentous Phycomycetes, especially the Saprolegniales and Peronosporales, is undoubtedly much the same as in the Siphonales. But the absence of chlorophyll and the greater delicacy of the filaments makes it more difficult to recognize the different regions of the protoplasm. There is an outer plasma membrane inside of which the granular material slowly moves in protoplasmic currents that may sometimes be observed in rapidly growing tips. Delicate strands which are the paths of streaming currents are beautifully shown in developing sporangia of the molds and the oögonia of the Saprolegniales and Peronosporales. The nuclei are undoubtedly carried by the protoplasmic movements, sometimes collecting in considerable numbers in growing regions of the filaments which always contain much dense protoplasm.

Another type of cœnocyte, and in some respects the most remarkable, is the plasmodium of the Myxomycete. These structures are too well known to need description here. We shall only refer to them as they help to break down an old theory that the cœnocyte is a compound structure composed of many energids, represented by the nuclei, which coöperate to make up the whole. The plasmodium and the protoplasmic mass inside the cellulose tubes of the Siphonales and Phycomycetes agree in all essentials of structure and mode of growth. The forward growth of the plasmodium, as is also true of the Amœba, begins with the prolongation of the outer plasma mem-

brane (hautschicht, ectoplasm) into a process (pseudopodium) which advances and is followed immediately by an inflow of the granular cytoplasm. And the growth of the filaments of the Siphonales and higher Phycomycetes is a pushing forward of the outer plasma membrane followed by the granular protoplasm, but this growth is slow because the plasma membrane is at all times under the restraint of a cellulose envelope.

Mention should be made of the remarkable cœnocytic zoöspores well known in Vaucheria and also described by Thaxter ('95*b*), for the Phycomycete Myrioblepharis. In Vaucheria the entire contents of the sporangium becomes transformed into an immense multinucleate zoöspore, the cilia being distributed in pairs above the nuclei. In Myrioblepharis the contents of a sporangium usually forms four large multiciliate zoöspores.

These zoöspores of Vaucheria have often been called compound zoöspores, and the idea has been expressed that they stand for the coöperative union of many hundreds of zoöspores (energids) represented by the nuclei and their respective pairs of cilia. And this explanation of the zoöspore of Vaucheria is a part of a broad view, formerly very largely held, that the cœnocyte is an assemblage of energids (uninucleate masses of protoplasm) coöperating in a fused structure.

The theory of the coöperative association of energids in a cœnocyte (Sachs) has been very much modified. While the nucleus and some other organs of the cell, such as groups of cilia, plastids, etc., are homologous with the same structures in uninucleate cells nevertheless the behavior of the cœnocyte is not the same as a group of coöperating protoplasmic units. The cœnocyte reacts to the usual stimuli in precisely the same manner as a uninucleate cell, and must be regarded as physiologically presenting no peculiarities over the latter structure excepting those of an increased bulk of protoplasm demanding a greater number of nuclei for its metabolic processes. The most important contribution presented by the cœnocyte to our knowledge of the physiology of the cell is the establishment of the plasma membrane as the region of the protoplasm responsive to the stimuli that determine the form assumed in growth. The constant shifting of the nuclei and plastids in the movement of the

granular protoplasm eliminates them as structures immediately concerned with the form of a cell or organ thus limiting their functions more especially to metabolism.

6. The Cœnogamete.

The cœnogamete is a multinucleate sexual cell. The name was first applied by the author (Davis, :00, p. 307) to the remarkable multinucleate eggs of *Albugo bliti*, and the conception has been considerably extended since, as explained in his later writings on Saprolegnia (Davis, :03, p. 320–331) and on "The relationships of sexual organs in plants" (Davis, :04*b*). Stevens ('99) discovery of the multinucleate eggs of *Albugo bliti* opened a field of research that has been greatly extended in the past four years and which is likely to yield very important conclusions on the relationships and evolution of the Phycomycetes and Ascomycetes. Conditions similar to *Albugo bliti* were reported the following year by Harper, :00*b*, for Pyronema, and several later papers have described, with greater or less fullness, the structure and behavior of cœnogametes in some other Ascomycetes, types of the Peronosporales (species of Albugo) and in the Mucorales.

We shall not discuss the details of these investigations with their bearings upon the problems of phylogeny as this has become a very complicated subject and is treated elsewhere (Davis, :04 *a–b*), but merely describe the structure and behavior of cœnogametes so far as they are known to us.

Stevens and Harper both found that the multinucleate female cell of *Albugo bliti* and Pyronema was fertilized by the introduction of a large number of nuclei from the antheridium. These sexual nuclei paired off and fused, a male with a female, in the common mass of cytoplasm so that the fertilized cell finally contained a large number of fusion nuclei. A similar history was reported later by Stevens (:01), in *Albugo portulacae* and *Albugo tragopogonis*. These events have been so thoroughly studied that we know the processes of fertilization in the above forms as well perhaps as for any plant type.

The structure and especially the nuclear history of other

cœnogametes is less perfectly understood. The multinucleate character of the fusing gametes is well known, but the later distribution and fate of the sexual nuclei has not been followed, and it is by inference that we believe these cœnogametes to behave in essentially the same manner as those of Albugo and Pyronema.

Cœnogametes fall into two classes according as they involve all of the protoplasm contained within the mother-cell or only a portion of such protoplasm. The first group probably represents the simplest and most primitive conditions.

Cœnogametes of the first class are found in the Mucorales (Gruber :01) and in the Gymnoasceæ (Dale, :03). In these types the entire contents of the terminally formed sexual cells unite to produce the zygospore in the former group and the fertilized ascogonium in the latter, from which arises the system of ascogenous hyphæ.

Cœnogametes of the second class contain only a portion of the protoplasm in the mother-cell which is usually a terminal structure. The protoplasm that is not involved in the cœnogamete proper generally bears some important relation to the sexual element. Thus the periplasm of the Peronosporales assists in the formation of the wall of the oöspore and the conjugation tube of Pyronema becomes the path through which the contents of the antheridium enters the ascogonium. But in some forms the superfluous protoplasm is merely cut off from the cœnogamete as a sterile cell (Monascus). In Albugo and Pyronema the sterile and fertile portions of the protoplasm are so closely associated that the mother-cell really acts as a whole, very much as the simplest types of cœnogametes which shows the close relationships between the two. Moreover the antheridia of these forms are types of cœnogametes almost as simple as those of the molds or the Gymnoasceæ.

The cœnogamete is a type of sexual cell unknown in the animal kingdom and among plants is probably restricted to the Phycomycetes and Ascomycetes. The problems of its homologies and origin are very interesting.

The simplest types of cœnogametes (Mucorales and Gymnoasceæ) are cells situated at the ends of filaments in the same position as the sexual organs of the Siphonales. The mother-

cells of the more complicated cœnogametes (oögonia and antheridia) are also terminal cells. All of these sexual organs are multinucleate. In the Siphonales (Vaucheria excepted) all of the nuclei are functional gamete nuclei. This is also true of simplest types of cœnogametes, but in the more complicated forms (Albugo, Pyronema, etc.) large numbers of the nuclei degenerate or fail to function sexually in sterile accessory regions of the protoplasm. The same conditions of sexual degeneration are also found in the oögonia of Vaucheria (Davis, :04) and Saprolegnia (Davis, :03). The agreement of all of the structures mentioned above in structure and protoplasmic behavior seems to establish beyond question their common homology.

The problems of the origin of the cœnogametes are very difficult with the meager evidence at hand. The author believes that the simplest types have probably been derived from structures like the sexual organs of the isogamous Siphonales, which structures gave up the habits of forming uninucleate gametes and acting as cœnocytic units became multinucleate sexual elements. A physiological development very similar to such a change must have taken place in Peronospora and some species of Pythium when their conidia ceased forming zoöspores and took the habit of germinating directly by a tube. This view regards the cœnogamete as a cœnocyte derived from a protoplasmic structure that at one time produced a large number of independent sexual elements, represented in the cœnocyte by the numerous nuclei. Whether the higher types of cœnogametes (Albugo, Pyronema, etc.) have developed directly from the simpler forms or from levels of the heterogamous algæ, such as are illustrated by Vaucheria, are very complicated problems that cannot be treated here. They with other topics, mentioned above, have been considered in recent papers of the author (Davis, :03, ;04*a*, :04*b*). Cœnogametes are proving to be among the most interesting types of sexual cells in plants and research in this field is likely to prove very fruitful of results.

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(*To be continued.*)

THE AFFINITIES OF THE OPHIOGLOSSACEÆ AND MARSILIACEÆ.

DOUGLAS H. CAMPBELL.

THE last ten years have been notable for many important contributions to our knowledge of the pteridophytes, due in part to a more exact investigation of many forms already studied, but still more to a critical study of tropical types, which hitherto have been studied more or less superficially, owing to the difficulty of procuring suitable materials for complete investigations. The fossil forms have also yielded much important material for a better understanding of the affinities of some of the living ones.

The work has covered a wide field and comprises very valuable additions to our knowledge of the anatomy and development of many interesting types which were but imperfectly known before. These investigations have added materially to the data available for a critical comparison of the different groups, and we are in a much better position than ever before to understand the affinities of some of the more puzzling types of pteridophytes. It must be admitted, however, that the conclusions of botanists in regard to the relationships of certain groups are by no means entirely in accord.

There are two orders of ferns about whose relationships there has been a good deal of controversy, and it is the bearing of some of the recent investigations upon these relationships to which the writer would direct attention. The two orders referred to are the Ophioglossaceæ and the Hydropteridineæ, especially the Marsiliaceæ.

THE OPHIOGLOSSACEÆ.

The Ophioglossaceæ constitute a very natural family of fern-like plants, evidently closely related among themselves, but

whose affinities to the other pteridophytes have been much discussed. They are generally considered to belong to the Filicineæ, or ferns with which they agree in their general structure. The writer has expressed the opinion that the sporangium of Ophioglossum represents the lowest type found in the fern series. This conclusion is based upon the structure of the living forms, as the Ophioglossaceæ are almost unknown in a fossil condition, perhaps owing to the soft tissues which characterize them. These would hardly be preserved as fossils except under the most favorable conditions.

As is well known, the Ophioglossaceæ differ from the typical ferns in the position of the sporangia, which are borne upon a peculiar structure (sporangiophore) arising from the inner surface of the leaf, either directly from the lamina or from the petiole. The sporangiophore may be a simple spike with two rows of large sporangia scarcely projecting at all, or it may be much branched and the numerous sporangia quite distinct and even stalked. (Campbell, *Mosses and Ferns*, p. 296.) The former structure occurs in Ophioglossum, the latter in Botrychium and Helminthostachys. The simpler species of Botrychium, such as *Botrychium simplex* and *Botrychium lunaria*, form a transition between the type of Ophioglossum and the larger species of Botrychium and Helminthostachys, in which both the sterile and fertile leaf segments are much branched, and the free sporangia bear a certain resemblance to those of Osmunda or Angiopteris. It is possible that the latter types, or at any rate Osmunda, may have arisen from forms like Botrychium or Helminthostachys, through which they would be connected with the more primitive type of sporangium found in Ophioglossum.

Much the most important recent work upon the sporangia of these puzzling forms is that of Bower ("Studies in the Morphology of Spore-Producing Members"; *Phil. Trans.*, 1894–1903, 185–196), whose views as to the relationship of the Ophioglossaceæ differ radically from those of most students of the pteridophytes. He considers the whole spike of Ophioglossum as the equivalent of a single sporangium of Lycopodium, produced by growth and septation from an originally unilocular structure. He is not inclined to admit any direct relationship

between the Ophioglossaceæ and the true ferns, and thinks they are probably more nearly related — although very remotely — to the lycopods. In his most recent work (*loc. cit.* No. V, p. 253), however, he recognizes the importance of the decidedly fern-like character of the gametophyte and recedes somewhat from the extreme views expressed in the earlier paper. He seems still unwilling, however, to give up the homology between the sporophyll in Ophioglossum and Lycopodium. It is held that all the pteridophytes are reducible to a common strobiloid type, which is most clearly seen in the lycopods and Equisetaceæ, but which is believed to be recognizable in the ferns as well. With this view the writer has been unable to agree.

Bower thinks it inconceivable that a large-leaved type could originate directly from any conceivable form of bryophyte sporogonium, and therefore concludes that all the primitive pteridophytes must have been microphyllous. To the writer there seems to be no greater difficulty in assuming that a single leaf-like organ may have been developed at the base of the sporogonium (*Mosses and Ferns*, p. 515) than that a series of small leaves should be developed as eruptions from its surface. Why both forms may not have been developed quite independently is not clear, either from the evidence of comparative morphology, or from the fossil record. That a special assimilative structure, remotely comparable to a leaf, may originate from the base of the sporogonium is shown in many mosses, where the apophysis is of this nature. In certain species of Splachnum the apophysis assumes a relatively very large size, and is expanded into a disc which might almost be compared to a perfoliate leaf. Of course there is no question of a direct homology between the apophysis of a moss and the leaf of a vascular plant, but the fact is patent that the sporogonium of a moss may give rise to a special assimilating organ, and it is therefore quite conceivable that the progenitor of the large-leaved ferns may have arisen from some bryophytic type by an analogous formation of a special organ which became a true leaf subtending a sporogenous structure much as is actually seen in Ophioglossum.

That the Ophioglossaceæ represent an ascending series, as Professor Bower (Bower, *loc. cit.* No. 5, p. 233) believes, is

extremely probable; but that the lowest members of the series are to be connected with forms in any way like the Lycopodiaceæ appears to the writer exceedingly doubtful. The direct origin of a type like Ophioglossum from an Anthoceros-like prototype has been considered at length elsewhere (Campbell, — *loc. cit.*, p. 515) and will not be discussed further here.[1]

The numerous structural resemblances in both gametophyte and sporophyte between the Ophioglossaceæ and Marattiaceæ are too great to be passed over, and indicate a genuine relationship between the two. It seems to the writer that the importance of these obvious resemblances has been rather minimized by some recent authors, and it may be just as well to call attention afresh to some of the most striking ones.

Our knowledge of the gametophyte of the Ophioglossaceæ is now pretty complete, owing to the important researches of Jeffrey (The Gametophyte of Botrychium virginianum, *Proc. Canad. Inst.* V, 1898) and Lang (On the prothalli of Ophioglossum pendulum and Helminthostachys zeylanica, *Ann. Bot.* 16, 1902). The former has described in detail the prothallium of *Botrychium virginianum*, while Lang was fortunate enough to procure fairly complete material of *Ophioglossum pendulum* and *Helminthostachys zeylanica*, so that all three genera are represented. As might be expected, there is a good deal of similarity, this being most marked between Botrychium and Helminthostachys. All agree in having a subterranean prothallium which is destitute of chlorophyll, thus resembling the prothallia of certain species of Lycopodium. It is highly improbable that this condition is a primitive one, however, and too much stress cannot be laid upon it in making a comparison with the green prothallia of the Marattiaceæ, with which otherwise there is a close agreement, especially in the case of Ophioglossum. As some species of Lycopodium have a green prothallium, and chlorophyll has been found under certain circumstances in the pro-

[1] Since this paper was written there has been published by Bower (*Ann. of Bot.* Apr. 1904) an account of a remarkable species of Ophioglossum from Sumatra, in which the leaf consists simply of a long-stalked sporangiophore with scarcely a trace of the sterile segment. This interesting plant almost realizes the hypothetical form assumed by the writer as the ancestor of the ferns.

thallium of Ophioglossum (Mettenius — *Filices Hort. Bot. Lips*, 1856), it is extremely likely that the absence of chlorophyll is a secondary condition, and that so far as the prothallium is concerned, the Marattiaceæ approach more nearly the ancestral type than do the Ophioglossaceæ.

Both Jeffrey and Lang are agreed as to the essentially fern-

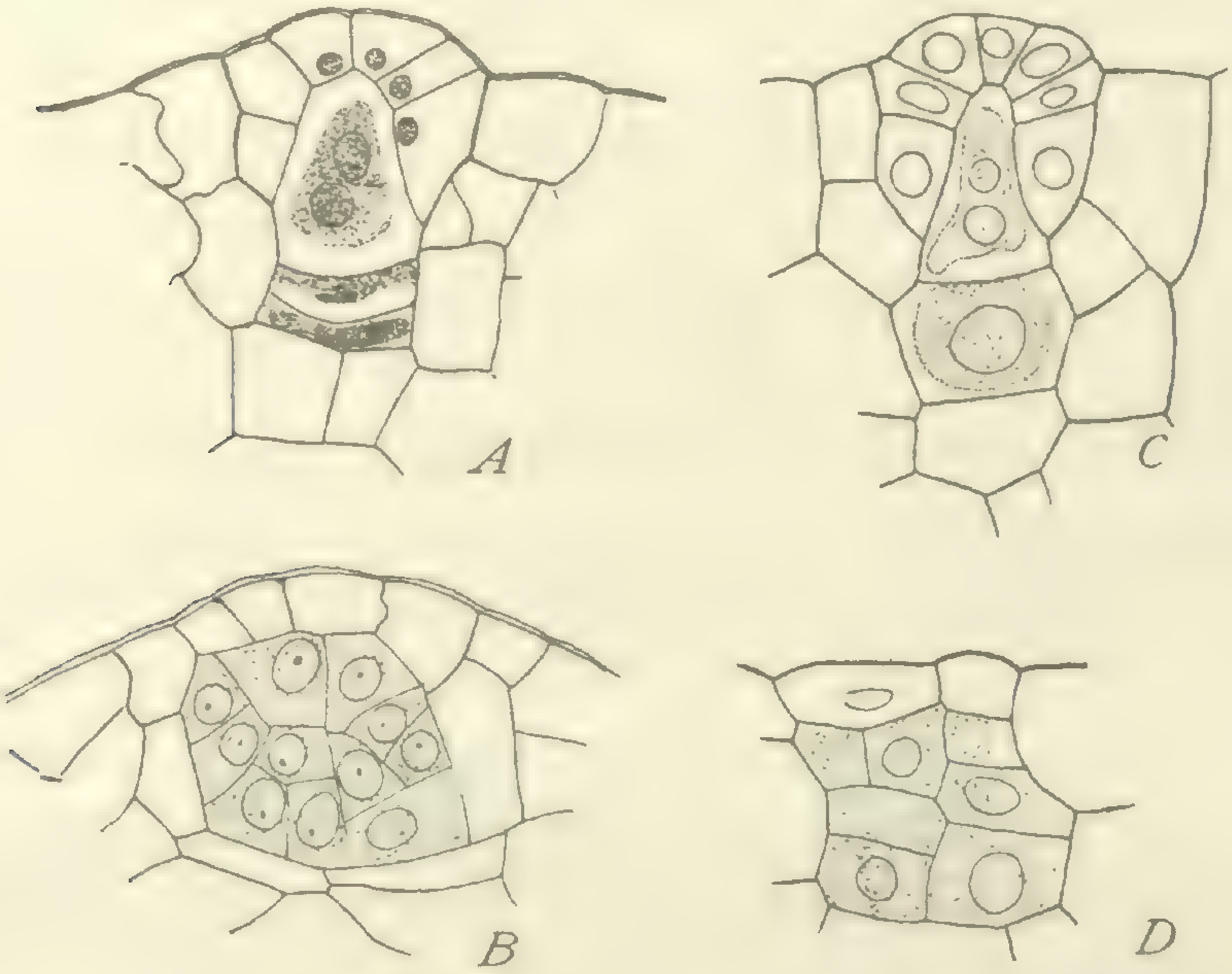

FIG. 1.—*A*, archegonium; *B*, young antheridium of *Marattia douglasii*, × 350. *C*, archegonium; *D*, young antheridium of *Ophioglossum pendulum*, × 250. *C*, *D*, after Lang.

like character of the prothallium. This is shown in its apical growth, strongly dorsiventral form, and especially in the reproductive organs, which in Ophioglossum (Fig. 1, *A*, *B*) resemble to an extraordinary degree those of Marattia. The large multiciliate spermatozoids are also entirely fern-like in form. When to the close resemblance in the sexual organs is added the marked correspondence in the development of the embryo, which is very similar to that of the Marattiaceæ and not in the least like that of Lycopodium, the case seems a very strong one.

There next remains to be considered the structure of the adult sporophyte. In most species of both Ophioglossum and Botrychium the stem is a short upright rhizome about which the leaves are spirally arranged. In *Ophioglossum pendulum*, however, and in Helminthostachys the plant is dorsiventral. Among the Marattiaceæ both types also occur. Marattia and Angiopteris are radial, Danæa is dorsiventral. Bower (*loc. cit.*,

p. 219) is inclined to consider the radial type as older than the dorsiventral, but as both types occur in both families under consideration, this has little bearing upon the question of their relationships.

In the structure of the apical meristems the Ophioglossaceæ are even more fern-like than the Marattiaceæ, as they regularly show a single tetrahedral initial in both stem and root. In this respect they resemble the leptosporangiate ferns more than they do the Marattiaceæ. In the very young sporophyte of the latter, however, the root shows a single apical cell which is replaced by a group of initials in the more massive roots of the older sporophyte.

The very complicated vascular system of the older sporophyte in the Marattiaceæ is undoubtedly associated with the massive stem. A study of the young plant shows that in the earlier stages there is a single cylindrical stele much like that which occurs in the adult rhizome of Helminthostachys and such leptosporangiate ferns as Gleichenia. This is considered by Jeffrey to be a primitive condition from which the more complicated arrangement found in the adult stem of the Marattiaceæ has been derived. The arrangement of the vascular bundles in the stem of Ophioglossum is much like that in the typical ferns, while Botrychium closely resembles Osmunda. (Jeffrey, "Structure of the Stem in the Pteridophyta and Gymnosperms," *Phil. Trans.* 195, 1902.)

The leaves of the Ophioglossaceæ, which are in some respects different from those of the typical ferns, nevertheless are much more like these than like either the lycopods or Equisetaceæ. The venation is not essentially different from that of the Marattiaceæ, and although there is never found the circinate form of the young leaf, so characteristic of the ferns, still in the larger species of Botrychium there is an approach to this which suggests that the coiling of the young leaf is connected with the very great development of the lamina of the leaf which characterize most ferns.

While the reticulate venation found in Ophioglossum is different from that in most ferns, still there are many ferns which show a very similar venation. Thus among the Marattiaceæ

there may be instanced Kaulfussia, whose venation is not very different from that of Ophioglossum, and possibly a further comparison might be made in the form of the leaf with the palmately lobed leaf of *Ophioglossum palmatum.* On the other hand, the venation of Agiopteris or Danæa is almost identical with that of Helminthostachys. (See Fig. 2.)

Farmer (Farmer & Freeman, "The Structure and Affinities of Helminthostachys," *Ann. Bot.* 1899) has referred to the stipules of the latter genus and thinks they are not directly compa-

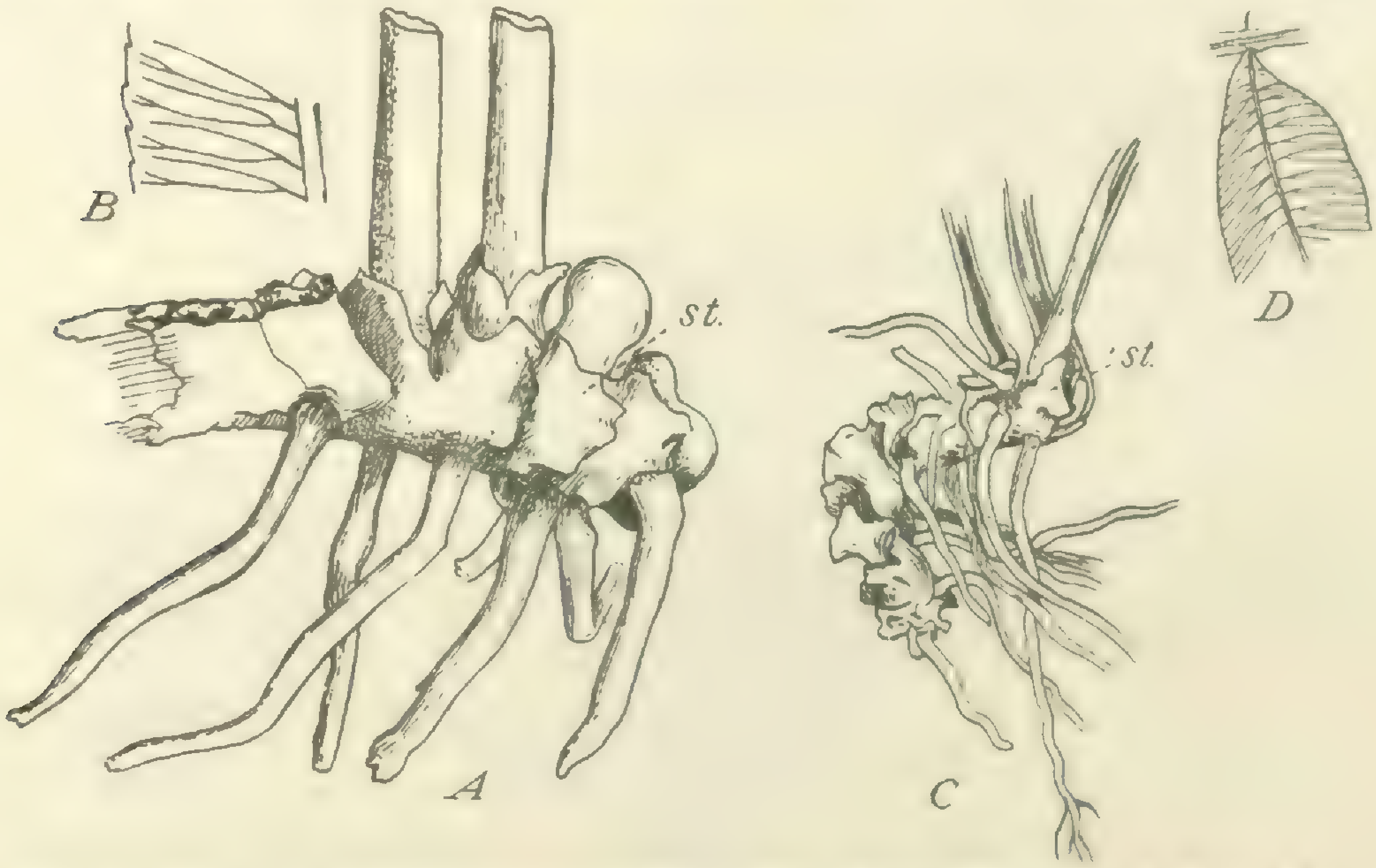

Fig. 2.—*A*, rhizome of *Helminthostachys zeylanica*, after Farmer; *B*, part of a leaflet of the same plant, showing the venation; after Hooker & Baker: *C*, Rhizome of *Danæa alata*, (reduced); *D*, base of leaflet showing venation; st., stipules.

rable to those of the Ophioglossaceæ, although it is not quite clear wherein the difference consists. There certainly seems to be no essential difference between the stipular structure at the leaf base in Botrychium (Campbell, *Mosses and Ferns*, p. 242) and those in Marattia or Danæa, although in the latter genera the stipules are more distinct. The development of stipular structures is especially marked in both Ophioglossaceæ and Marattiaceæ, while among the Leptosporangiatæ they are generally absent except in the Osmundaceæ, which are admittedly the nearest relatives among the Leptosporangiatæ to the eusporangiate ferns.

The markedly dorsiventral rhizome of Danæa is strongly sug-

gestive of that of Helminthostachys (Fig. 2, *A*, *C*), and the position of the leaves and roots is much the same. The cylindrical stelar tube with relatively small foliar lacunæ in Helminthostachys may perhaps be compared to the stele in the young rhizome of Danæa, which, according to Jeffrey, is of much the same type. (Jeffrey, *loc. cit.*, pp. 120, 121.)

The most marked histological difference between the Marattiaceæ and the Ophioglossaceæ is perhaps the occurrence of conspicuous mucilage ducts in the former. These are, however, also wanting in the other ferns. The circinate form of the young leaves is probably associated with the great development of the lamina of the leaf, but is certainly a difference of some importance.

To the labors of Bower we owe by far the most important contributions to our knowledge of the development of the sporangium that have been made for many years. These enable us to make a detailed comparison of all the developmental stages in each group, and a careful study of his descriptions and figures of the two groups in question have led me to a somewhat different result from that reached by him.

The progression from the sporangial spike of Ophioglossum to the much branched sporangiophore of Botrychium or Helminthostachys, with its numerous distinct sporangia, is comprehensible enough; but the relation of the sporangiophore of the Ophioglossaceæ to the sporangia of the other pteridophytes is not so obvious. Bower believes (*loc. cit.*, p. 250) that all pteridophytes may be reduced to the strobiloid type, this being reduced to a single sporophyll in Ophioglossum. As we have stated elsewhere, this theory seems hardly satisfactory when applied to the ferns, however probable it may appear for the other pteridophytes. The comparison of the sporangial spike of Ophioglossum to the single sporangium of Lycopodium appears rather improbable, and it seems more in accordance with the facts to consider it an entirely distinct development, derived directly from the whole upper part of the sporogonium of the ancestral form.

Bower's very complete account of the sporangia in Ophioglossum and the Marattiaceæ suggests a possible point of con-

tact between the two groups. In the very peculiar *Ophioglossum palmatum*, there may be several nearly sessile sporangiophores borne near, or actually upon, the margin of the large palmately lobed sterile segment of the leaf. Among the Marattiaceæ

FIG. 3.—*A*, leaf of *Ophioglossum palmatum*, showing the position of the numerous sporangiophores, *sp.*, —after Bower; *B*, part of a sporophyll of *Danæa alata*, showing the elongated synangia, *sp.*; × 2.

Danæa shows a marked resemblance to Ophioglossum in the arrangement of the loculi in the greatly elongated synangia, which almost completely cover the lower surface of the contracted sporophylls. A study of the development of the sporangia in the two, to judge from Bower's account and figures, shows a close resemblance in many particulars.

Bower thinks that the elongated synangium of Danæa has been secondarily derived from a circular one, like that of Kaul-

fussia, but there is no certain evidence, either morphological or geological, that the type found in Danæa may not be the older. While a direct comparison of the sporangiophore of the existing species of Ophioglossum with the synangium of Danæa would be hardly justifiable, still it is conceivable that synangia of the type of Danæa might have originated from the complete adhesion to the surface of the sterile leaf segment of a series of small sporangiophores not so very different from those actually found in *Ophioglossum palmatum* (Fig. 3). If the primitive character of the synagium of Danæa is admitted, it is easy to trace the origin of the marattiaceous types by the expansion of the leaf lamina. Bower suggests that the primitive type of Marattiaceæ probably had an undivided leaf like that of *Danæa simplicifolia*, with scattered round sori similar to those of Kaulfussia. We agree with this except as to the character of the sori, which we believe were quite as probably like those of the actual *Danæa simplicifolia.*

In comparing the two families, Ophioglossaceæ and Marattiaceæ, it is clear that they closely resemble each other in the character of the reproductive organs and embryo, and also in the apical growth and dorsiventral form of the gametophyte. The position of the archegonia and the absence of chlorophyll are undoubtedly associated with the subterranean life of the gametophyte.

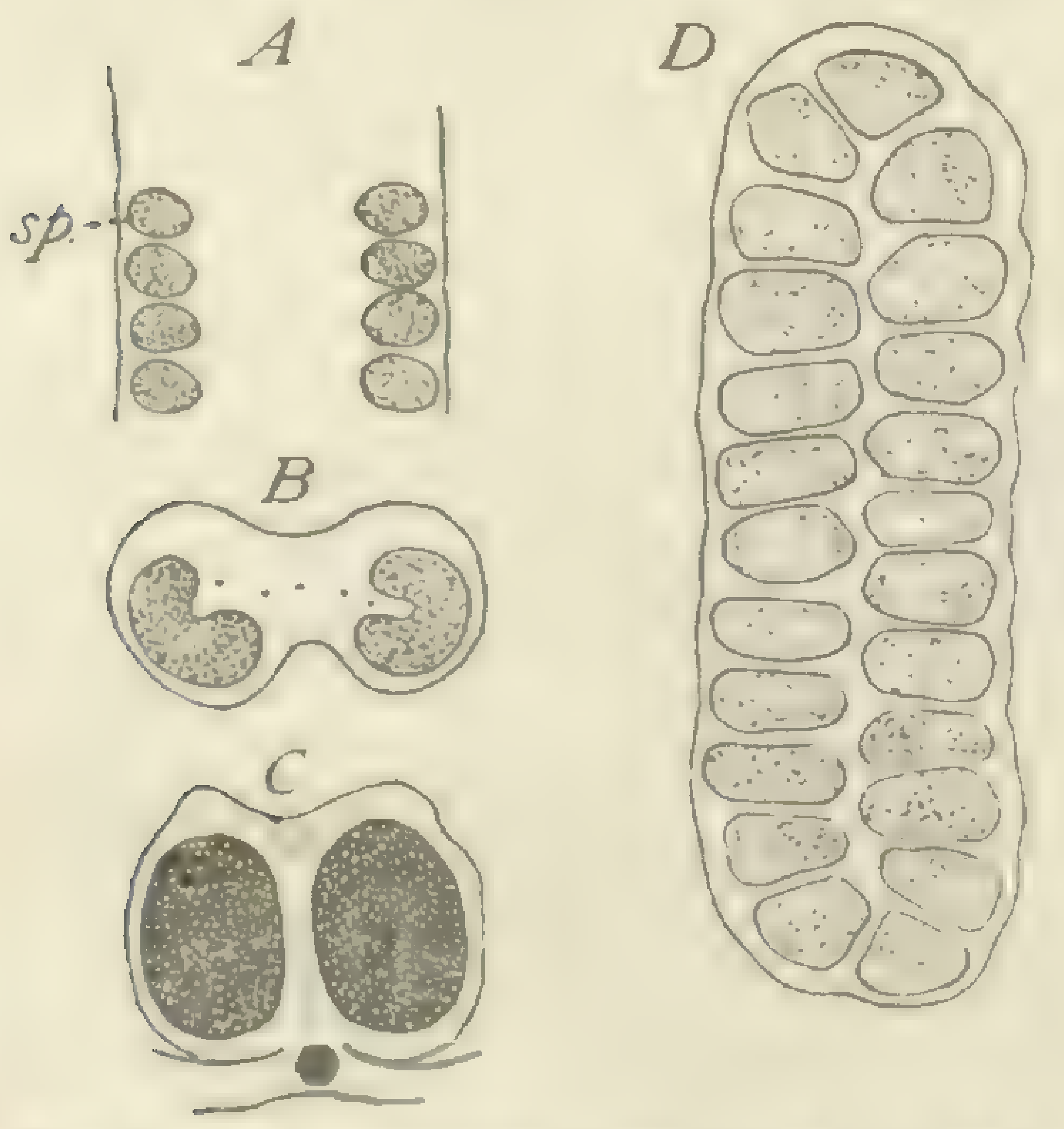

FIG. 4 — *A*, longitudinal section of part of the sporangiophore of *Ophioglossum pendulum*, × 2; *B*, cross-section of the same; *C*, cross-section of the synangium of *Danæa alata*, × 15; *D*, longitudinal section of the same.

While in the sporophyte such differences as the coiled vernation of the leaf, and presence of mucilage ducts in the Marattiaceæ must be taken into account, the two orders nevertheless agree in the general morphology of both stem and leaf, including the venation of the leaves, while in regard to the apical growth of the stem and root, the Ophioglossaceæ are more like the higher ferns than are the Marattiaceæ. Finally,

whether or not the possibility of a direct connection between the two is admitted, there is no question of the strong resemblance between the sporangia of Ophioglossum and Danæa. In view of all these facts, we can see no valid reason for removing the Ophioglossaceæ from their association with the ferns, and we believe that their association with the Marattiaceæ among the eusporangiate ferns is entirely justified.

The Marsiliaceæ.

That the Marsiliaceæ are directly allied to some group of homosporous leptosporangiate ferns is apparent; but there has been little attempt to connect them directly to any of the existing ferns. The writer (*loc. cit.*, p. 421) has suggested a comparison

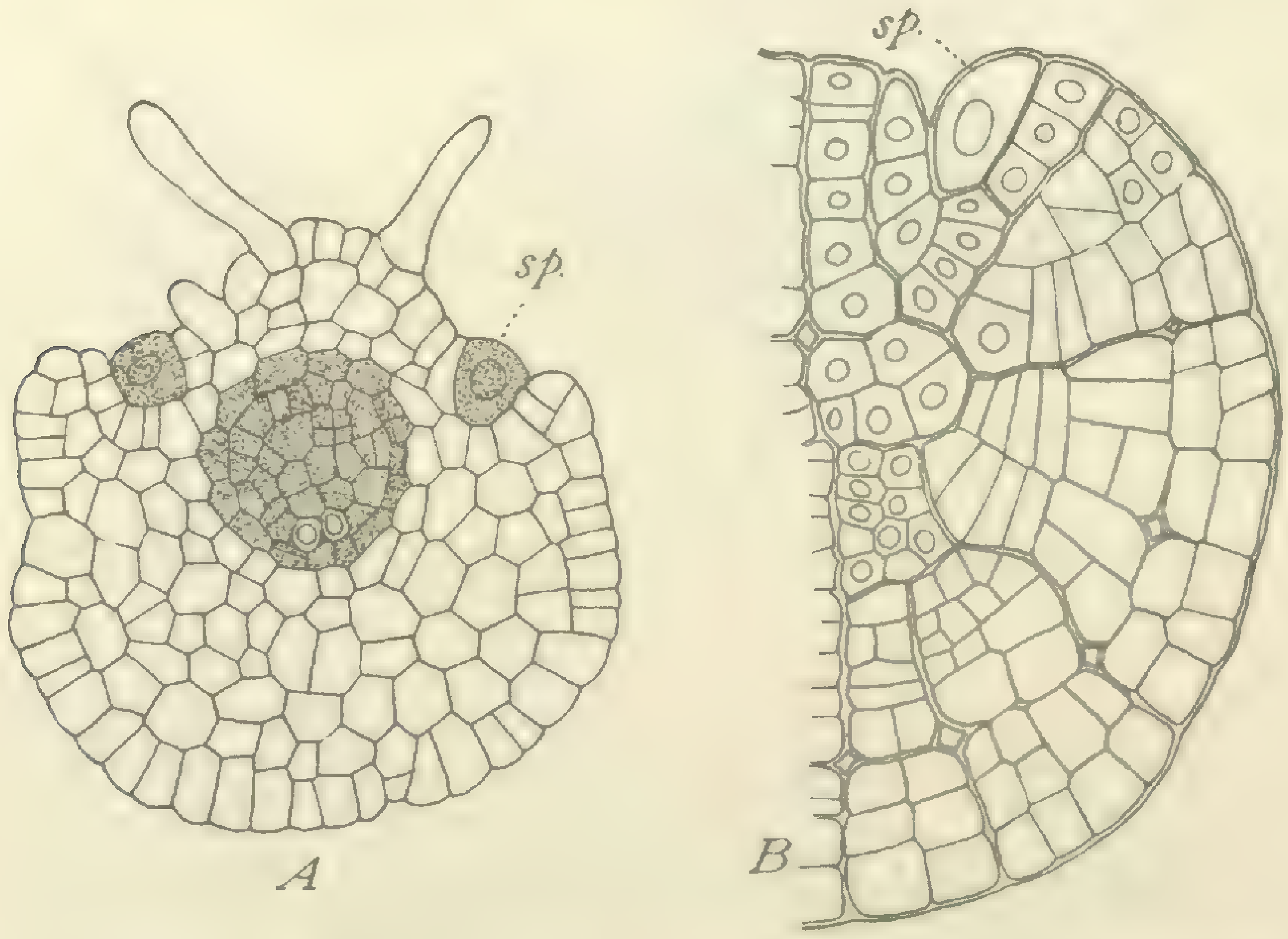

Fig. 5.—*A*, cross-section of a fertile leaf-segment of *Schizæa pennula*, highly magnified; *sp.*, sporangium mother-cell — after Prantl; *B*, cross-section of very young sporocarp of *Marsilia quadrifolia*, × 500, after Johnson. The marginal cell, *sp.*, gives rise to a row of sporangia.

with the peculiar Ceratopteris, and has also compared the antheridium with that of the Polypodiaceæ.

The more recent work of Belajeff ("Die männlichen Prothallien der Wasserfarne," *Bot. Zeit.*, 1898) on the antheridium, and of Johnson ("On the leaf and sporocarp of Marsilia," *Ann. Bot.* XII, 1898) ("On the leaf and sporocarp of Pilularia," *Bot. Gaz.* XXVI, 1898) and Gœbel (*Organographie der Planzen*,

Part II, 1900) upon the sporocarp, have suggested a somewhat different affinity, and it was thought worth while to look into the evidence carefully, supplementing it by a direct comparison of such material as was available.

Gœbel has called attention to the similarity between the young sporocarp of Marsilia and the fertile leaf-segment of Schizæa. Johnson's studies on the sporocarp of both Marsilia and Pilularia bear out this, and a comparison with Prantl's figures of the

FIG. 6.—*A*, sporophyll of *Aneimia hirsuta*, showing the very conspicuous fertile pinnæ, *sp.*; *B*, Plant of *Mearsilia salvatrix*, with the long-stalked sporocarps, *sp.*, after Sachs.

young sporophytes of Schizæa emphasizes the marked resemblance between the two (Fig. 5). Johnson does not admit the foliar nature of the sporocarp; that is, he does not believe the capsule is homologous with the leaf lamina, a view which has been expressed by the writer, and which is supported by most students of the subject. A comparison of the developing fertile segment of the leaf of Schizæa, however, shows that at the time the first rudiments of the marginal sporangia appear, there is no more trace of a lamina than in a corresponding stage of the sporocarp in Marsilia. In short, the structure of the very

young sporocarp of Marsilia and the fertile leaf segment of Schizæa is remarkably similar; moreover, the origin of the sporangia from originally marginal cells is noteworthy.

The origin of the sporocarps in the Marsiliaceæ, however,

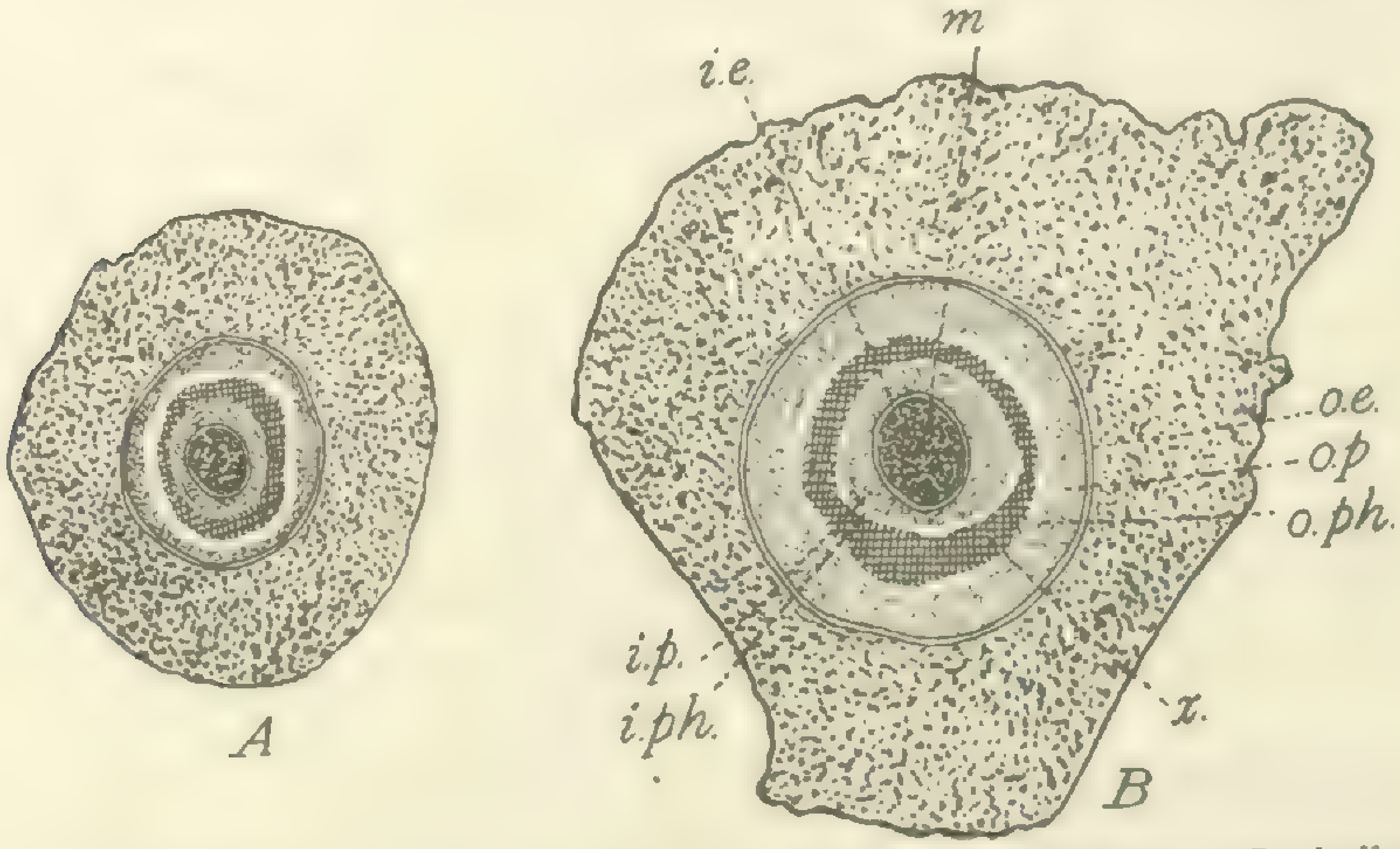

FIG. 7.—*A*, cross-section of the rhizome of *Marsilia vestita*, × about 15; *B*, similar section of the rhizome of *Aneimia hirsuta*. The outer cortical tissue is composed in both of brown sclerenchyma; the tubular stele encloses a medulla also composed of sclerenchyma; the stele has an outer (*o. e.*) and an inner (*i. e.*) endodermis, outer (*o. p.*) and inner (*i. p.*) pericycle; outer (*a. ph.*) and inner (*i. ph.*) phlœm; and a central xylem (*x*).

is different from that of the fertile leaf-segment in Schizæa, but finds a close counterpart in the allied genus Aneimia (Fig. 6) where the remarkably developed fertile pinnæ bear much the

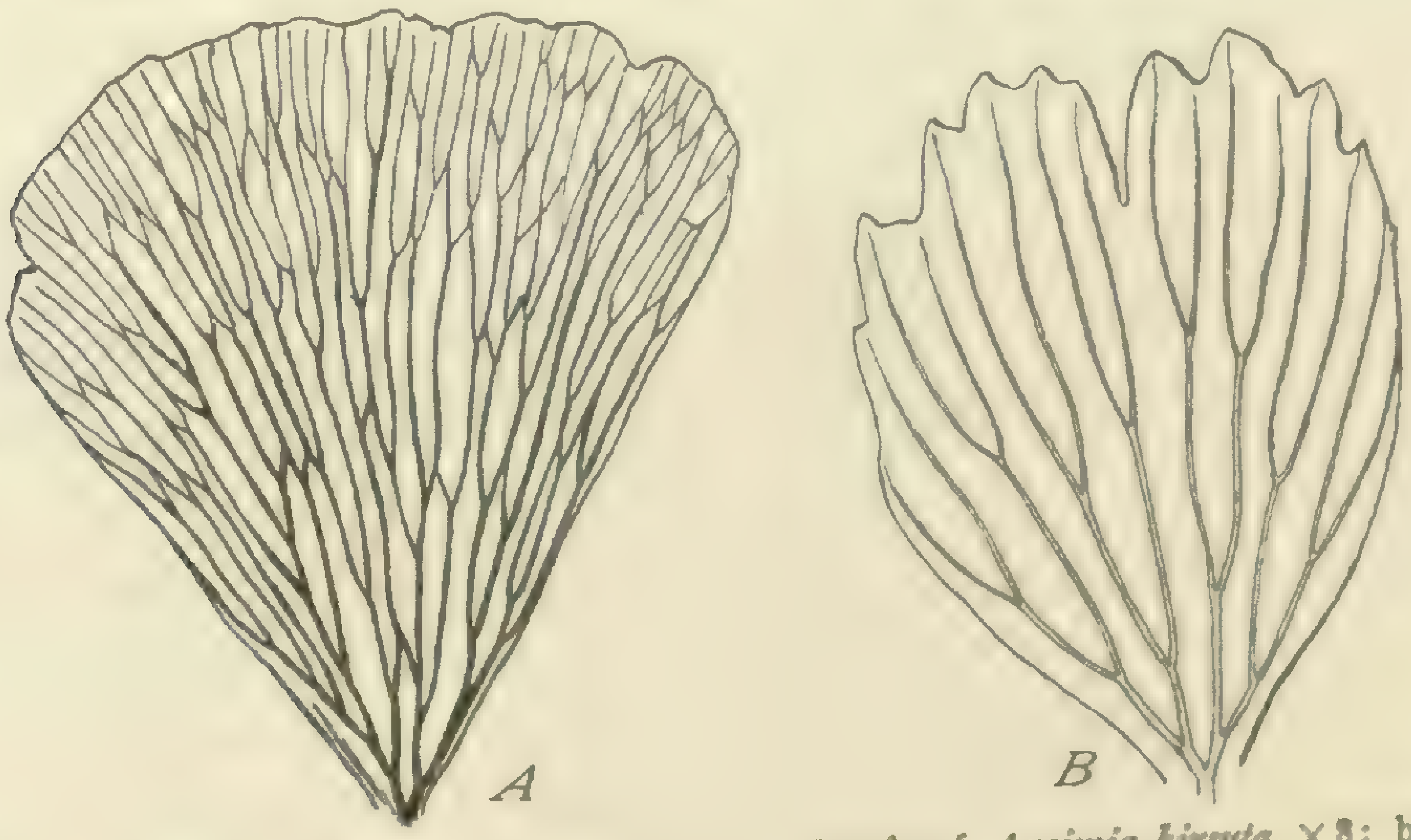

FIG. 8.—*A*, leaflet of *Nearsilia vestita*, × 10; *B*, pinnule of *Aneimia hirsuta*, × 8; both show a strictly dichotomous venation.

same relation to the rest of the leaf, that the sporocarp does in Marsilia. The pinnate form of the sporocarp in Marsilia and the dichotomous sterile segment, are comparable to what obtains

in some species of Schizæa, where the leaf is dichotomously divided, but the fertile segments are pinnate.

A comparison of the vegetative organs of the Marsiliaceæ and Schizæaceæ shows equally marked resemblances. The creeping rhizome of Marsilia and Pilularia is remarkably similar to that of Schizæa and certain species of Aneimia (Fig. 7), as may be clearly seen from the figure. The leaves also show interesting resemblances. Thus the filiform leaf of Pilularia finds its exact counterpart in the sterile leaves of *Schizæa pusilla*, while the four-lobed leaf of Marsilia is comparable to such species as *Schizæa pennula*, with dichotomously branched lamina. The venation in Schizæa and Aneimia is characteristically dichotomous, closely resembling that of Marsilia. Except in Lygodium, the pinnate venation found in the majority of the ferns does not occur among the Schizæaceæ.

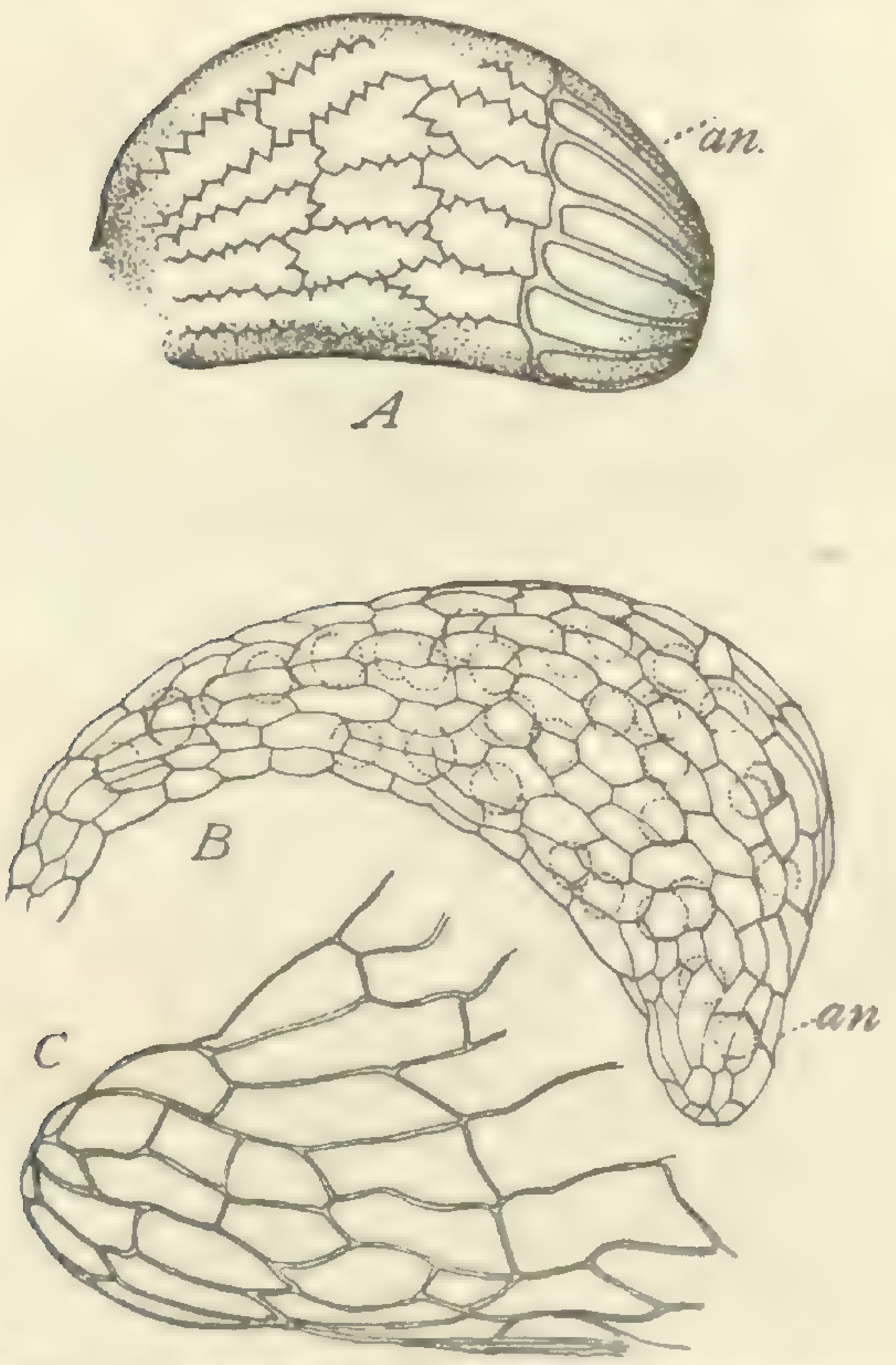

Fig. 9.—*A*, sporangium of *Schizæa pennula*, showing the apical annulus, *an*. × 45, (after Prantl), *B*, sporangium of *Pilularia Americana*; the apical region suggests the annulus of Schizæa; *C*, apical region, more enlarged.

So far as I am aware, no direct comparison of the sporangia in the two families has been made, although the early stages of the sporangium have been carefully studied. The Schizæaceæ differ from all the other ferns in the very peculiar form of the sporangium which is strongly oblique and has a terminal annulus. The sporangia of *Pilularia americana* and *Marsilia vestita* were examined, and it was found, especially in the case of the former, that the sporangia resembled strongly those of the Schizæaceæ. In Marsilia the closely packed microspore rendered it difficult to make out the form of the parietal cells, but in Pilularia the spores are widely separated and the form of the parietal cells is easily seen when the sporangia,

after placing them in water for a short time, are treated with alcohol to check the swelling of the mucilaginous cell walls which otherwise are soon completely destroyed. The oblique form of the sporangium is especially conspicuous in Pilularia (Fig. 8, *B*), and the arrangement of the cells near the apex is very suggestive of the annulus of Schizæa, although of course in these aquatic plants, no hardening of the annulus cells takes place.

This remarkable correspondence in the structure of the sporangium, taken together with the other close structural resemblances, justifies the assumption of a not very remote relationship between the Schizæaceæ and Marsiliaceæ.

It may be added that this view would tend to confirm the contention of Belajeff, that in the male gametophyte there are two antheridia, and not a single one as the present writer has held. The antheridium of the Schizæaceæ [1 2] is relatively simple in structure, and might very well be compared to each of the groups of sperm-cells in Marsilia, with its two peripheral cells.

[1] Bauke — Berträge zur keimungsgeschichte der Schizæaceæ *Prings. Jahrb.* XI, 1878.

[2] Britton, E. G. & Taylor,—A life history of Schizæa pusilla. *Bull. Torrey Bot. Club*, XXVIII, 1901.

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THE EMBRYOLOGICAL DEVELOPMENT OF THE SKELETON OF THE HEAD OF BLATTA.[1]

WILLIAM A. RILEY.

OUR knowledge of the embryological development of the sclerites of the head of insects is very meager. With but few exceptions the subject has been treated in the most incidental manner and the observations are few and scattered. This is due not only to the fact that attention has been directed to the more general features of insect embryology, but is due also to a lack of systematizing of our knowledge of the structure of the head of the adult insect and to the difficulty of determining the limits of the sclerites before they become firmly chitinized.

Of all the students of insect embryology, Heymons ('95 and '97), Janet ('99), and Comstock and Kochi, (:02), are the ones who have devoted the most attention to this subject and these workers differ radically in their conclusions.

It was in hopes of determining the conditions in one of the more generalized of the pterygote insects that I undertook the study of the embryological development of the skeleton of the

[1]Contribution from the Entomological Laboratory of Cornell University.

head of *Blatta germanica.* This was proposed by Prof. Comstock and to him I am indebted for many suggestions.

In the choice of an object for this study I was guided by the desire to select one of the more generalized forms and one which at the same time would afford an abundance of material. Both of these conditions seemed to be met by *Blatta germanica.* Though undoubtedly highly specialized in some respects, the cockroach is regarded by many students as the most primitive of our pterygote insects. I believe that in this respect one of the Plecoptera would have been more valuable, but as regards abundance of available material it would be difficult to select a form more satisfactory than is Blatta.

On the other hand, as objects of study the embryo of Blatta present certain difficulties which are accentuated in the course of the work. Of these there are "die ausserordentlichen technischen Schwierigkeiten" which Cholodkowsky has so emphasized. These are due primarily to the great mass of yolk, which becomes so brittle as to make it almost impossible to secure complete series of sections by ordinary methods. A more serious difficulty in the work under consideration was the small size of the cells and the indistinctness of the invaginations of the body wall. Of the latter, Wheeler ('89, p. 349) says: "In *Blatta* the formation of the nervous system in its earlier stages cannot be clearly seen from the exterior. The same holds true of the small tracheal invaginations, though several pairs, especially those of the thorax and basal abdominal rings, may be seen on the pluræ in good preparations before revolution. Still they are so much less distinct than in *Doryphora* that I have given them little attention."

The Primitive Segments of the Head.

The question of the number of segments in the body of the perfect insect early attracted the attention of entomotomists. As the history of the development of our knowledge of the number entering into the structure of the head has been very fully discussed by Comstock and Kochi (:02), I have but little to add to their account.

As early as 1839, Newport discussed this question in considerable detail. He believed in the "correctness of the opinions advanced by Savigny and others, that the organs of manduction are the properly articulated members of distinct segments and are perfectly analogous to the proper organs of locomotion." He attributed the conflict of views to a "too exclusive examination of the head in perfect insects, without reference to the corresponding parts in the larva."

It was thus early realized that it is to the ontogenetic record that we must appeal for a settlement of the question. Unfortunately Newport chose as the basis of his study the larva of *Musca vomitoria*, a form so highly specialized as to be worthless for this purpose. His evidence regarding the possible presence of a fifth segment must therefore be rejected. The value of his conclusion that there were at least four segments was due to his acceptance of the criterion proposed by Savigny.

Zaddach ('54), believed that six segments entered into the composition of the head. Of these the first was the ocular, while the third was the second antennal segment. His evidence regarding the presence of the latter, however, was based upon the erroneous conclusion that in the phryganids the larval antennæ represented the second pair of the Crustacea, and that they were later replaced by the definitive antennæ of the adult, which corresponded to the antennules of the Crustacea.

In 1858 Huxley also discussed the mooted question from the view point of embryology. With characteristic thoroughness and penetration he not only treated of the embryology of an insect, Aphis, but compared its development with that of Crustacea and Arachnida. Granting that the presence of paired appendages was indicative of an equal number of segments, he argues that the absence of the appendages does not necessarily imply the absence of the segment. "No one will pretend that it is so in the abdominal and thoracic regions." In conclusion he proposes the hypothesis "that in the Articulata the head is normally composed of six somites, which are all fully developed only in Podopthalmia, Stomapoda, and some Branchiopoda, while in other Crustacea some one or more of the preoral somites is more or less abortive, and in Arachnida and Insecta the

appendages of the first somite are sessile and those of the second or third undeveloped."

I shall have occasion to revert to this paper of Huxley's, for, as we shall see, he devoted considerable attention to a consideration of the development of the head, and brought out some facts of prime importance.

Packard ('66), believed that the insectean head was composed of seven segments. In 1870, in the second edition of the *Guide to the Study of Insects*, he gives a table of these segments and their appendages. He believed the segments to be a *first ocellary*, *second ocellary*, *opthalmic*, *antennary*, *mandibular*, *first maxillary*, and a *second maxillary* or *labial*. In addition to these seven he includes a hypothetical first segment whose tergal parts give rise to the labrum, epipharynx, and clypeus.[1] Thus at this time he regarded the insectean head as composed of eight primary segments.

In 1871, however, Packard presents evidence to show that the ocelli and the compound eyes do not represent appendages. "Accordingly," he says, "we seem forced to the belief that the head of the hexapodous insect consists of but four segments, *i. e.*, the second maxillary, the first maxillary, and mandibular segments behind the mouth opening and the antennary, or first and preoral segment situated in front of the mouth." This view he reiterates in 1883. In 1898 he tabulates six segments.

One of the most recent workers to approach this subject is Janet ('99). Basing his conclusions largely on a study of the musculature of the adult Vespa, this worker states that the so-called primary head segment — the protocerebral segment of authors — is in reality composed of four segments and that therefore the head of an insect is made up of not less than *nine* segments, all of which were primitively postoral. According to Janet these segments are:

1° Le somite du gésier	ou	somite proto-stomodæal
2° Le somite œsophagien	ou	somite deuto-stomodæal
3° Le somite clypéo-pharyngien	ou	somite trito-stomodæal

[1] "The tergal parts (*i. e.*, the labrum, epipharynx, and clypeus) situated in front of the ocelli, are left out in enumerating the seven segments as they are not supposed by the author to belong to either of those segments." *L. c.* p. 20.

4°	Le somite du labre	ou	somite proto-cérébral
5°	Le somite antennaire	ou	somite deuto-cérébral
6°	Le somite post-antennaire	ou	somite trito-cérébral
7°	Le somite mandibulaire	ou	somite proto-gnathal
8°	Le somite maxillaire	ou	somite deuto-gnathal
9°	Le somite labial	ou	somite trito-gnathal

From the embryological view point Janet sees support for these conclusions in the development of the sympathetic nervous system. He considers "the nervous system of the stomodæum (or the unpaired sympathetic system) as being simply the morphological prolongation on the ectodermic stomodæal invagination, of the chain of the central system." The untenability of this view has been pointed out by Heymons, (:00), who has devoted especial attention to the study of the development of the sympathetic system, and whose argument, therefore, carries especial weight.

Of the work of Patten, Wheeler, Viallanes and Folsom, the excellent résumé by Comstock and Kochi leaves little to be said. These last writers accept Folsom's conclusion as to the presence of seven primitive segments, and agree with him that the appendages of the superlingual segment may be represented in the Orthoptera by a pair of small sclerites lying behind the lingua, within the mouth cavity. Neither Heymons nor Wheeler[1] accept this view. As regards the condition in the cockroach, I have only the negative evidence that there is wholly lacking a trace of a ganglion belonging to this segment. The position of the above mentioned sclerites is such as to make them readily susceptible of explanation on purely mechanical grounds, as secondary structures. Though Folsom's work was done on Anurida, and his corroborative evidence was drawn from a study of other Collembola, it is not to be expected that we should find such a fundamental difference between the Apterygota and the Pterygota.

[1] In a forthcoming paper, which Dr. Wheeler has kindly allowed me to anticipate by the above statement, he very fully and conclusively presents the arguments against such a view.

The General Features of the Formation of the Head of Blatta.

The changes during the first six days [1] of the embryonic life of Blatta lead to the formation of the ventral plate, the blastodermic thickening which represents the first rudiment of the germ band. This extends along about two-thirds of the ventral surface of the egg, beginning at about one-fourth of the length of the egg from its cephalic end.

The newly formed germ band is not an evenly developed structure, but there are to be seen, on each side, groups of rapidly proliferating cells. These active cells give rise to an indistinct segmentation in the earlier stages of the germ band. This was noted by Cholodkowsky ('89), who says, (p. 91): "However, when I say that the young germ band of Blatta gives no indication of cross divisions I do not mean by that that there are no traces of metamerism. Very early when the germ band is still very imperfectly marked off from the surrounding undifferentiated blastoderm, one may observe a noteworthy grouping of its cells around certain points which are none other than the centers for the formation of the future appendages."

Heymons ('95), has correctly interpreted this description of Cholodkowsky's as referring to certain formative centers in the undifferentiated blastoderm, which by their extension and fusion give rise to the germ band. A similar method of formation of the germ band of Astacus had already been pointed out by Reichenbach ('86). That Cholodkowsky was not clear as to the nature of these centers is evident not only from his reference to them as the precursors of the appendages, but also from his Figure 2, which shows an embryo of about ten days, in which the mouth parts and thoracic appendages are already prominent, while there is to be seen "die beginnende Gruppirung der Zellen für die Anlagen des ersten Paares von Abdominalfüssen."

[1] Cholodkowsky ('91), states that on account of the peculiarity of ovoposition, the age of the embryos of Blatta is not easily determined. As an illustration of this, I have found that there may be considerable variation in the degree of development of the embryos of a single capsule. However, the few observations I have made have, in the main, confirmed Wheeler's approximations, and I have followed him in determining the ages of the embryos studied.

An interesting fact is that, as pointed out by Heymons ('95b), the cephalic lobes arise from three pairs of these centers of proliferation, which very early fuse. Wheeler found that two such centers entered into the formation of the lobes of Xiphidium. The presence of the three pairs would preclude Cholodkowsky's idea that these centers represent future appendages. On first thought it might seem that their presence confirms Janet's view as to the compound nature of the preoral region. Janet believes, however, that there are three segments lying cephalad of the cephalic lobes, and that these do not fuse with the lobes, but in the later stages are invaginated with the stomodæum. It is evident that the formative centers of the cephalic lobes lend no support to that view. It has been suggested that they might represent the three segments whose ganglia enter into the formation of the brain. That this is not the case is shown from the fact that these areas precede the definite formation of the germ band, and that their fusion and consequent obliteration has taken place long before the deuto- and tritocerebral segments have united with the protocerebral segment.

It is during the seventh day, after the appearance of the blastoporic thickening of the caudal end, that there becomes prominent a pair of thickenings laterally placed at the cephalic end of the germ band (Fig. 1, *c. l.*). These thickenings represent the cephalic lobes, which are destined to play a most important rôle in the formation of the head capsule. From the first they are connected with the germ band. Of an independent development, such as described by Will ('88) for Aphis and by Heider ('89) for Hydrophilus, I find no indication in Blatta.

FIG. 1. — The germ band of seventh day. The cephalic lobes *c. l.* are indicated × 120.

During the eighth day of embryonic life the most striking change is the appearance and very rapid development of the amnio-serosal folds, — phenomena which have been described in detail by Wheeler. The cephalic lobes develop rapidly, and during the first half of the ninth day they become prominently demarcated from the strap-like trunk region. The embryo in this stage covers about half of the ventral face of the egg, being somewhat

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logues à celui que nous décrivons maintenant qui a décidé la plupart des embryologistes à considérer, à tort croyons-nous, l'antenne comme un membre post-buccal." (p. 289.)

Viallanes was influenced in his interpretation by his studies of the nervous system of the adult, in which the deutocerebrum, the ganglion of the antennal segment, is clearly pre-oral, as is also its commissure.

More recently, Comstock and Kochi (: 02) have challenged the commonly accepted view. Believing that the clypeus "represents the median field of the sternite of the antennal segment," they argue that a study of the figures given by authors describing a post-oral position of these appendages "shows that while a line connecting the two antennæ would pass in some cases behind the mouth it is by no means so clear that the basal part of the rudiment of the antennal sclerite does not abut against the procephalon. In fact, the very figures given to support the view that the antennæ are post-oral in the early embryo support the opposite view." (p. 31.)

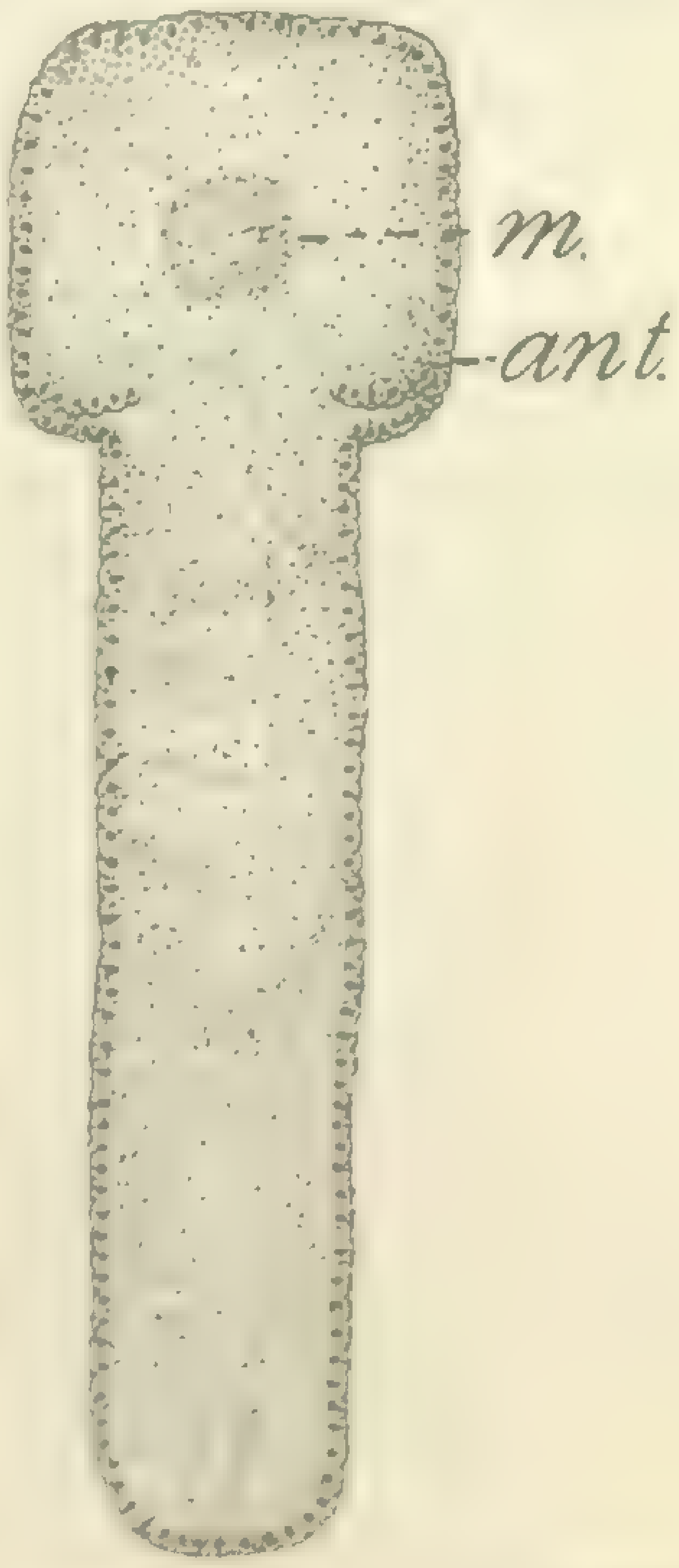

Fig. 2 — The ventral aspect of an embryo of about nine days. The antennæ *ant.* have just appeared, while the stomodæum (*m.*) is but indicated by a slight thickening of the cells. × 501.

A study of Blatta has served to confirm the view of Zaddach. At the time of the first appearance of the antennæ the stomodæal invagination has not yet manifested itself. Its position is marked, however, by an area of rapidly proliferating cells (Fig. 2, *m.*). The antennal rudiments are clearly caudad of this area, and are thus at their earliest appearance post-oral (Fig. 2, *ant.*). They increase rapidly in size, and at a stage but slightly later than that represented in Fig. 2, they lie caudo-laterad of the newly formed stomodæum. It is at this stage that they were studied by Viallanes. Very soon they are pushed more markedly post-orally, and it is in this stage that they have usually been figured (Fig. 3, *ant.*).

From the view point of comparative anatomy we have in Apus strong evidence of the original post-oral position of the antennæ.

Lankester thought that in this form the antennæ of the adult were innervated from subœsophageal ganglia. Though this has proven to be incorrect, Pelseneer ('85) has shown that the antennal ganglia of the adult, though associated with, are histologically perfectly distinct from those of the archicerebrum, and that they are perfectly homologous with the ganglia of the ventral cord.

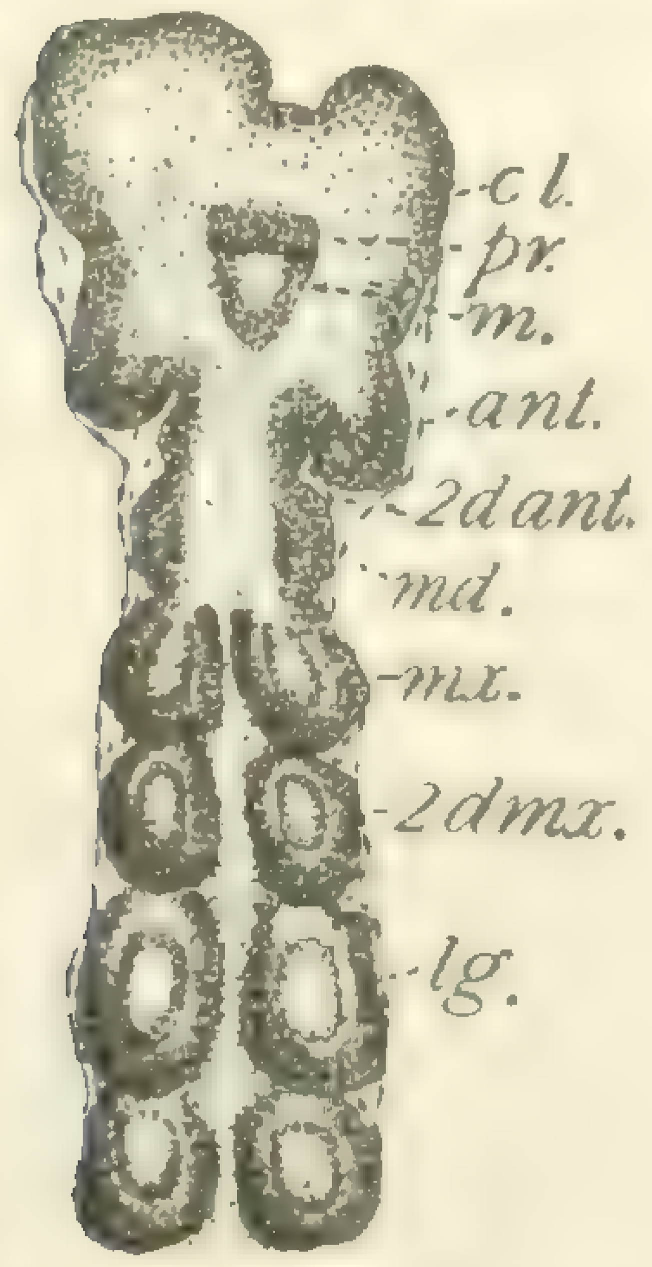

Fig. 3.— Embryo late in the tenth day. The antennæ lie laterad of the stomodæal opening. The procephalon (*pr.*) lies cephalad of the opening. Between the antennæ (*ant.*) and the mandibles (*md.*) lie the second antennæ (*2d ant.*). × 80.

By the end of the ninth day there are to be seen, in addition to the antennal rudiments, those of the thoracic appendages, which are distinctly outlined, while those of the mouthparts are merely indicated. This is the stage figured by Wheeler ('89, Fig. 44). Wheeler found that in many embryos, as in the one which he figures, "one or, more rarely, both antennary lobes are temporarily bilobed." This he thought might be due to a temporary reversion, 'tending to show that the antennary lobes originally gave rise to two pairs of appendages which were perhaps homologous with the two pairs of antennæ in the Crustacea.' In embryos but slightly more advanced I, also, have seen indications of this bilobulation. Believing that the antennæ of insects are not to be homologized with those of the annelids but, rather, are homodynamous with the other appendages, I should regard this temporarily bilobed condition as a possible reversion toward a biramous condition of the appendage.

The next notable change is the appearance, during the tenth day, of the mouth and of the rudiment of the procephalon. The mouth is not invaginated from within the latter, but, as is shown by Figure 3, lies caudad of it.

There has been much discussion concerning the origin of this rudiment of the procephalon which, by many, is spoken of as merely that of the labrum. A number of observers have reported that in certain forms it originates as a paired structure (Hydrophilus, Kowalevsky, '71, Heider, '89, Graber, '90; *Bombyx mori*, Tichomiroff, '82; Pieris, Gastropacha, Zygæna, Graber,

'90; Hyalotoma, Graber, '90; Chalicodoma, Carrière, '90, Bürger, '97). Kowalevsky, Patten, Carrière, and others maintain that not only does this structure arise from paired rudiments, but that it represents a fused pair of appendages. Bürger in his edition of Carrière's notes, does not commit himself to the latter view.

On the other hand a greater number of species have been noted in which the procephalon is, from the first, unpaired. Among these are included a number of Apterygota (see Folsom, :00, pp. 93–96), while of the Pterygota may be mentioned Aphis (Huxley, '58); Apis (Grassi, '84); Œcanthus (Ayers, '84); Forficula (Heymons, '95); Mantis (Viallanes, '91); Blatta (Cholodkowsky, '90); *et al.* Heymons has emphasized the fact that the place of origin of the labrum, *between* the two halves of the nervous system rather than laterad of them, fundamentally distinguishes this structure from the true appendages.

Especial attention was directed to this point in Blatta on account of finding an embryo in which the procephalon was quite clearly in two distinct halves. A study of a large number of other preparations of the same stage failed to duplicate this, though in some there was to be seen a slight mesal constriction. As the embryo first mentioned was otherwise distorted I am inclined to regard the appearance of the procephalon as abnormal, and to agree with Cholodkowsky that in Blatta its rudiment is unpaired.

Fig. 4 — Lateral aspect of an embryo a little older than the preceding. × 80

By the end of the tenth day the embryo has increased considerably in length, and the mouth part appendages are all distinct. In an embryo of 1.5 mm. length, the ocular and antennal segments, which at this time constitute the head of the embryo, measured 275 μ, while the mouth part region was 350 μ in length, their relative extent being thus as 11 : 14. The 1st and 2nd maxillæ are subequal and have relatively the same situation upon the germ band. The mandibles are considerably smaller, but are equally distinct (Fig. 4).

A striking feature of embryos of this period is the relation

of the mandibles to the antennæ. They are separated by a space much greater than that which separates the mandibles from the 1st maxillæ. This appearance, which in Hydrophilus proved so puzzling to Heider, is due to the presence of the so-called "intercalary," "Vorkiefer," "premandibular," or "tritocerebral" segment. As the evidence all tends to show that this segment is the homologue of the second antennal segment of the Crustacea, it should be designated either so or as the *tritocerebral* segment rather than by the indefinite and non-commital term "premandibular."

Wheeler ('93) was the first to demonstrate in Anurida a pair of vestigial appendages, which bear to its ganglion the same relation as do the other appendages to the ganglia of their respective segments. Wheeler's work has been abundantly confirmed by workers on the embryology of the Apterygota, Uzel ('98) and Folsom ('99) having determined that in certain forms these appendages persist even to the adult stage.

Though these results have been generally accepted as applying to the Apterygota, embryologists have been unwilling to accept the scant evidence of the presence of such vestigial appendages in the Pterygota. As long ago as 1870 Bütschli observed in the embryo of Apis a paired rudiment just behind the mouth, which, as he said, "sich fast wie ein Paar innerer Antennen ausnimmt." Bütschli himself did not regard this structure as homologous with the other appendages. Grassi ('84) also noted these appendages, but contrary to Bütschli, who thought that they fused to form a transitory under lip, Grassi states that they quickly disappear without leaving a trace. Moreover, he went farther than Bütschli in comparing them to antennæ, for, as Heider has pointed out, he says, "Il primo paio d'arti boccali, che ha un'esistenza effimera, può forse paragonarsi ad un paio d'antenne degli artrapode" (p. 57). Carrière ('90) described similar rudiments for Chalicodoma, and his statements were verified by Bürger ('97). On the whole, however, insect embryologists discard the above evidence and agree with Heymons ('95 b) who says of the tritocerebral segment, "Sein rudimentär Charakter gibt sich hauptsächlich darin zu erkennen, dass sich an ihm niemals Extremitäten entwickeln. Dies gibt wenigstens, so weit wir bisher wissen, von den pterygoten Insecten."

In the face of these opinions it may seem somewhat venturesome to assert that in Blatta there are evidences of the presence of such appendages. And yet, I believe that the facts warrant this conclusion. In embryos of the eleventh day, in favorable specimens there are to be seen between the antennal and the mandibular rudiments, in the region occupied by the tritocerebral ganglion, small but distinct thickenings of the hypodermis (Fig. 4, *2nd ant.*). Moreover, these are to be detected in both cross and longitudinal sections (Fig. 5), and bear to the ganglion of the tritocerebral segment the same relation which we should expect of appendages. To be sure, not every hypodermal thickening is to be interpreted as the rudiment of an appendage. Since, however, the thickenings under consideration occur not only in one but in several preparations, since they occur in the location we should expect for such appendages and do not occur between the other pairs of appendages, and since, lastly, they bear the expected relation to the ganglia of the second antennal segment, I see no other interpretation than that they represent vestiges of appendages such as are still developed in some of the apterygote insects.

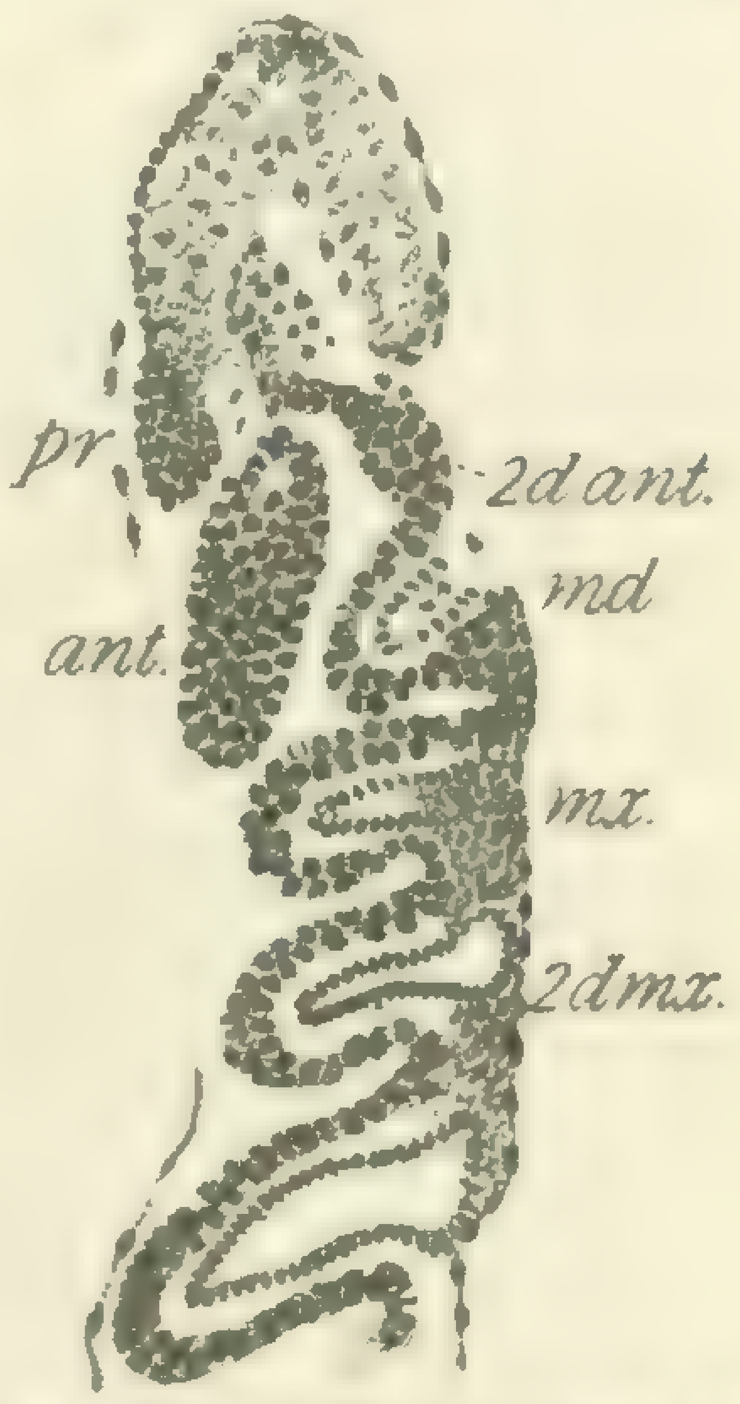

Fig. 5. — Longisection of an embryo of eleven days. × 106.

The mouth-part appendages rapidly increase in size, and early in the eleventh day the length of the 1st maxillæ considerably exceeds that of the second maxillæ, while a little earlier these appendages were subequal. Measuring from the caudal angle to the apex, we find the length of the mandibles to be about 55 μ, that of the 1st maxillæ 96 μ, while the 2nd maxillæ are but 70 μ. There is no trace of lobulation in any of the mouth parts.

The procephalic rudiment has become prominent and, in the latter part of the eleventh day, appears as a button-shaped swelling overlying the mouth. In surface views the mouth can be seen through the rudiment, lying slightly caudad of its center. It is this appearance which has led to the incorrect statement that the mouth develops *in* the procephalon. In embryos of

this age it will be seen that the antennæ are migrating forward. They have increased in length so as to almost completely overlie the mandibles.

FIG. 6. — Embryo of about thirteen days showing antennal sclerites (*a. s.*) × 80.

The procephalon increases rapidly in size and pushes caudad over the mouth and between the antennæ. In many specimens there is to be noted a constriction of its caudal portion, while the mesal notch of the caudal margin is also distinct.

Early in the twelfth day are to be seen signs of the lobulation of the 1st and 2nd maxillæ. I find no indication of the lobes of these appendages arising from separate, isolated centers, as Heymons ('95a) has described.

It has been stated that the mandibles of Blatta are always simple. I was interested to find that in a few embryos of twelve to thirteen days they appear to be feebly trilobed. This agrees with the condition in Œcanthus, as described by Ayers (p. 24). Korotneff ('81) also represents the mandibles of Gryllotalpa as feebly trilobed (see his Fig. 6), though he says nothing about it in the text.

FIG. 7. — 2nd maxilla of embryo of about thirteen days, showing lobulation. × 120.

Throughout the series it is evident that there is not a perfect fusion of the antennæ with the cephalic lobes, but the point of origin of these appendages is separated from the lobes by a constriction which demarcates a more or less definite area of attachment for the antennæ. This may be seen in Figure 6.

FIG. 8. — 2nd maxillæ of an older embryo (about fifteen days) showing the mesad migration. × 120.

The lobulation of the 2nd maxillæ is well shown by Figure 7, which shows one of these appendages from an embryo about thirteen days old. Their mesad migration proceeds rather slowly, until during the fifteenth day they present the appear-

ance shown in Figure 8. They have not yet fused, but the future labrum is clearly outlined. In the meantime they have also migrated forward, so that the space which formerly separated them from the 1st maxillæ has been considerably reduced, and in lateral view the 2nd maxillæ are more or less hidden by the first pair.

About this time there appears a prominent invagination lying cephalo-mesad of the base of the mandible, close to the mandibular ganglion. This lies under the antennæ, but can be seen by focusing below that appendage or by removing it (Fig. 9, *a.t.*). In the same embryos there are prominent ten pairs of tracheal invaginations on the pluræ of the meso-, and metathorax and the first eight abdominal segments. For the prothorax there is a pair of slight and indistinct invaginations which have escaped the attention of previous workers on Blatta. It should be noted that the location of the above mentioned mandibular invaginations is in no wise comparable to that of the tracheæ. In addition to these invaginations there are in the mouth-part region three other pairs — one pair at the cephalo-lateral angle of the mandibles, one between the mandibles and the maxillæ, close to the caudo-lateral angle of the mandibles, and one cephalo-laterad of the base of the 2nd maxillæ. The last pair of invaginations is difficult to detect, for they are smaller, their lumen is not prominent and is frequently hidden by the caudal margin of the 1st maxillæ. It is shown in Figure 10, *p. t.* The invaginations lying laterad of the mandibles form tendons for the mandibular muscles. The rôle of the first and the last pairs in the formation of the tentorium or endoskeleton of the head will be discussed later.

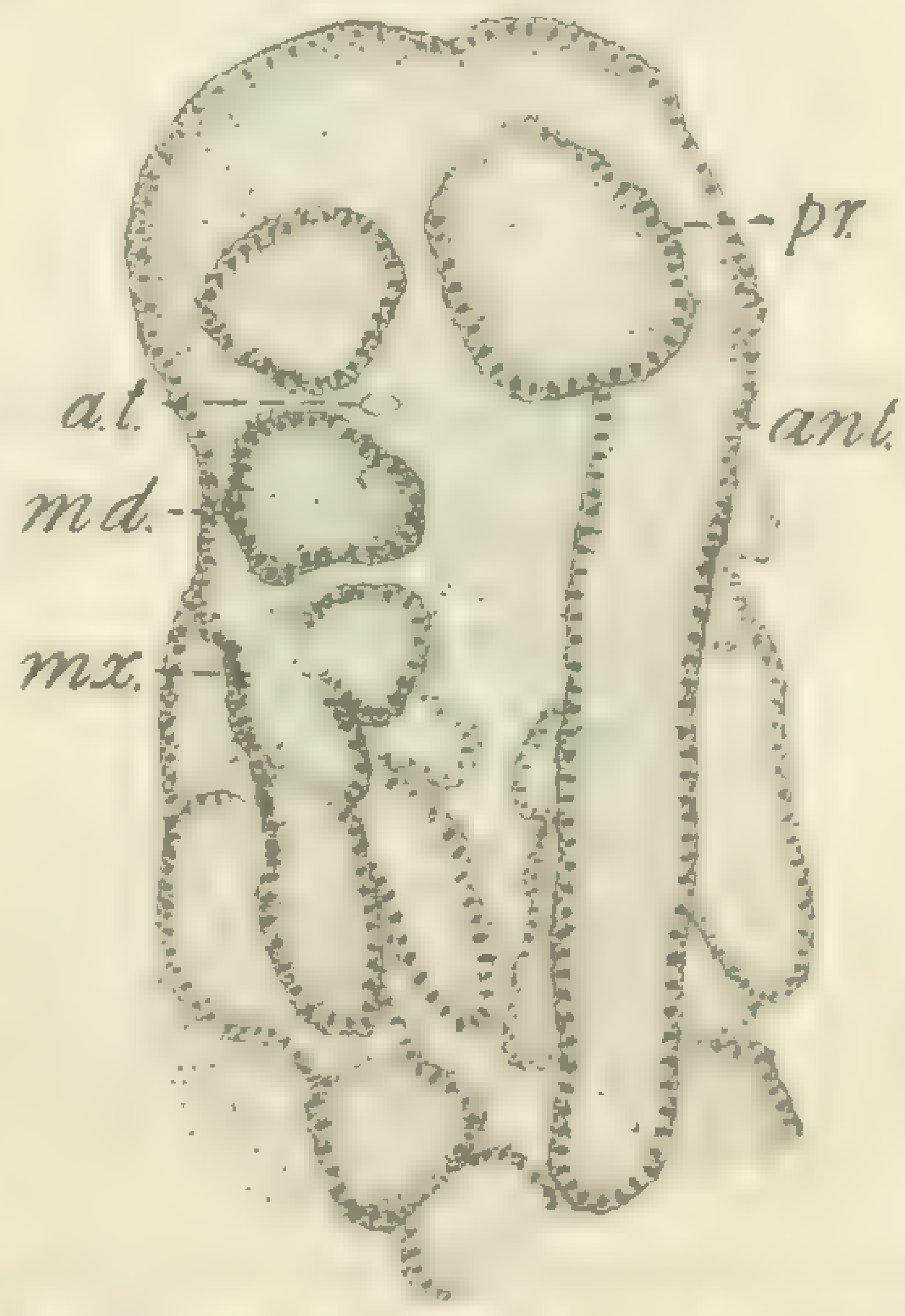

Fig. 9. — Embryo of about fourteen days with right antenna removed, showing the location of the anterior tentorial invagination (*a. t.*) × 80.

Up to this period the length of the mouth-part region has considerably exceeded that of the combined ocular and antennal segments. Thus, as we have seen, in an embryo of about eleven

days the latter region measured 275 μ in length as compared with 350 μ for the mouth-part region. In an embryo at the close of the twelfth day the antennæ have moved forward until the anterior section measures but 200 μ. The mouth-part region, owing to the loss of the tritocerebral segment and the reduction also taking place in the 2nd maxillary segment, measures 280 μ. A comparison early in the fourteenth day shows that the two regions are approximately equal in length. This, as we should suppose from the above, is due not so much to an increase in the size of the anterior region, as to a reduction of the mouth-part region, due to the cephalad migration of the mouth parts. The developing pronotum of the prothorax is pushing rapidly forward, and is limiting the pleural region of the maxillary segments (Fig. 10, *pn.*).

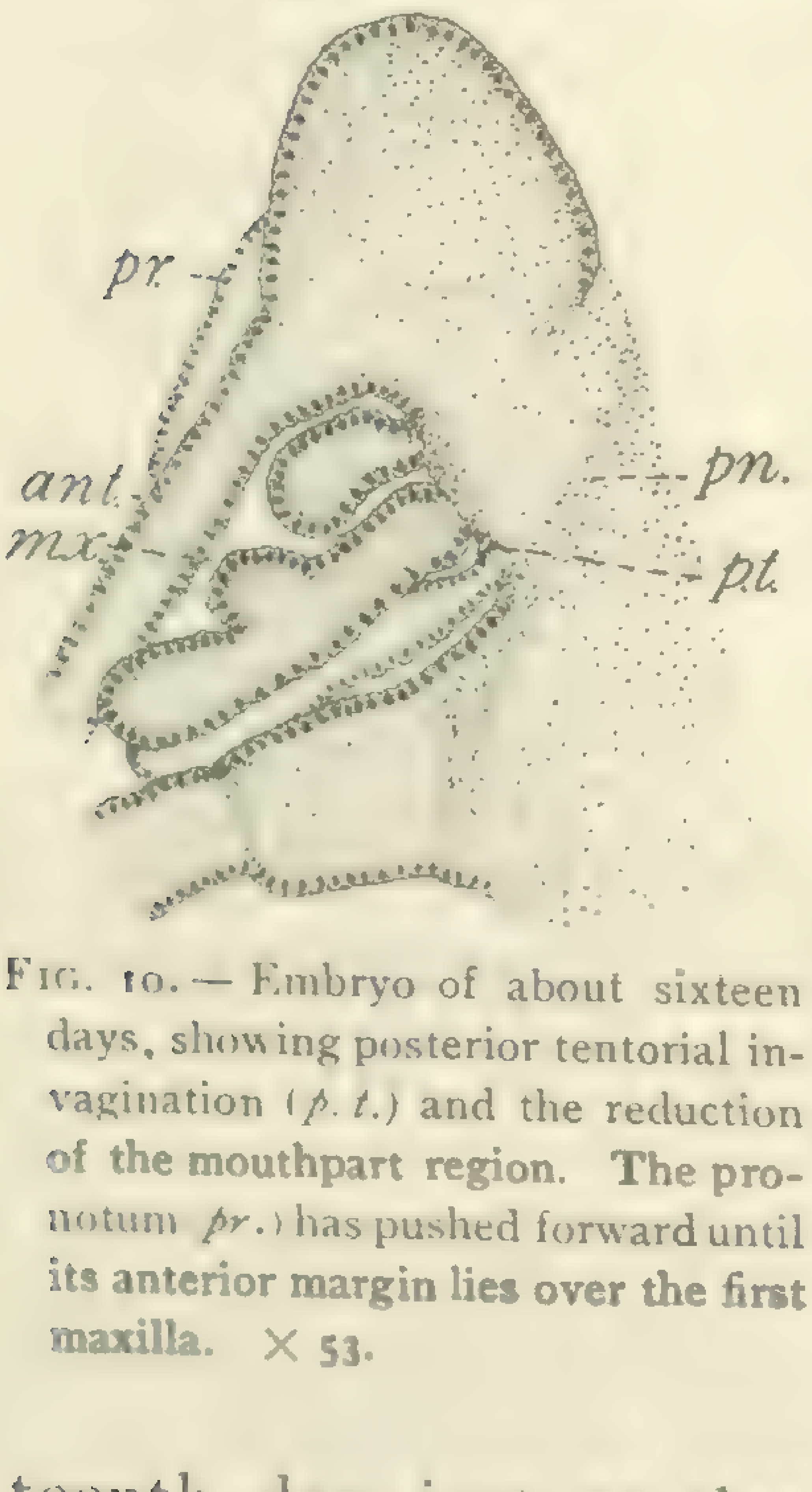

FIG. 10. — Embryo of about sixteen days, showing posterior tentorial invagination (*p. t.*) and the reduction of the mouthpart region. The pronotum (*pr.*) has pushed forward until its anterior margin lies over the first maxilla. × 53.

During the sixteenth day there occurs the series of changes which Wheeler ('89) has described as the revolution of the embryo. This is a period of very rapid growth, and at its close there has been completed the circumcrescence of the yolk by the embryo.

At about the beginning of the sixteenth day, just as these changes have commenced, the conditions do not differ markedly from what I have just described.

The reduction of the mouth-part region is rapidly progressing, the length of the anterior measuring 200 μ as compared with 160 μ for the mouth-part region. The pleural region of the prothorax has extended forward until its most cephalic point lies over the base of the 1st maxillæ, while its indistinct spiracular invagination lies over the base of the 2nd maxilla. The cephalic lobes have extended back until they lie well over the base of the mandibles. The 1st maxillæ greatly exceed the 2nd, which have all but fused to form the labium.

In ventral view of embryos about this age the appendages completely hide the sternal region; but on carefully dissecting

away the antennæ and the procephalon, it may be seen that the sternites of the mandibular and 1st maxillary segments have fused, and form a well marked area lying between their respective appendages (Fig. 12, *hyp.*). We shall refer to this again, in the discussion of the development of the sclerites.

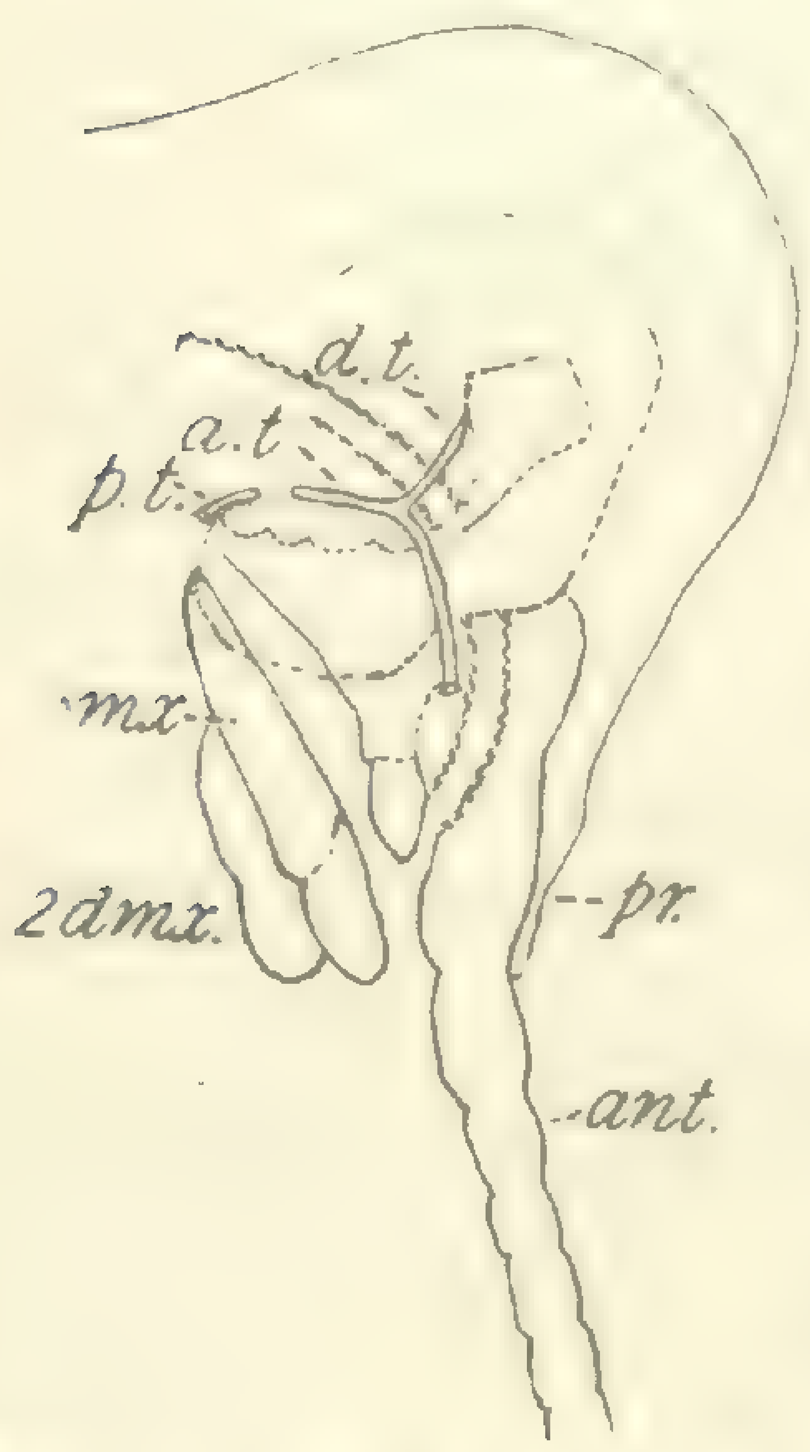

FIG. 11. — Diagram showing the arms to the tentorium in their relation to the nervous system and mouth parts.

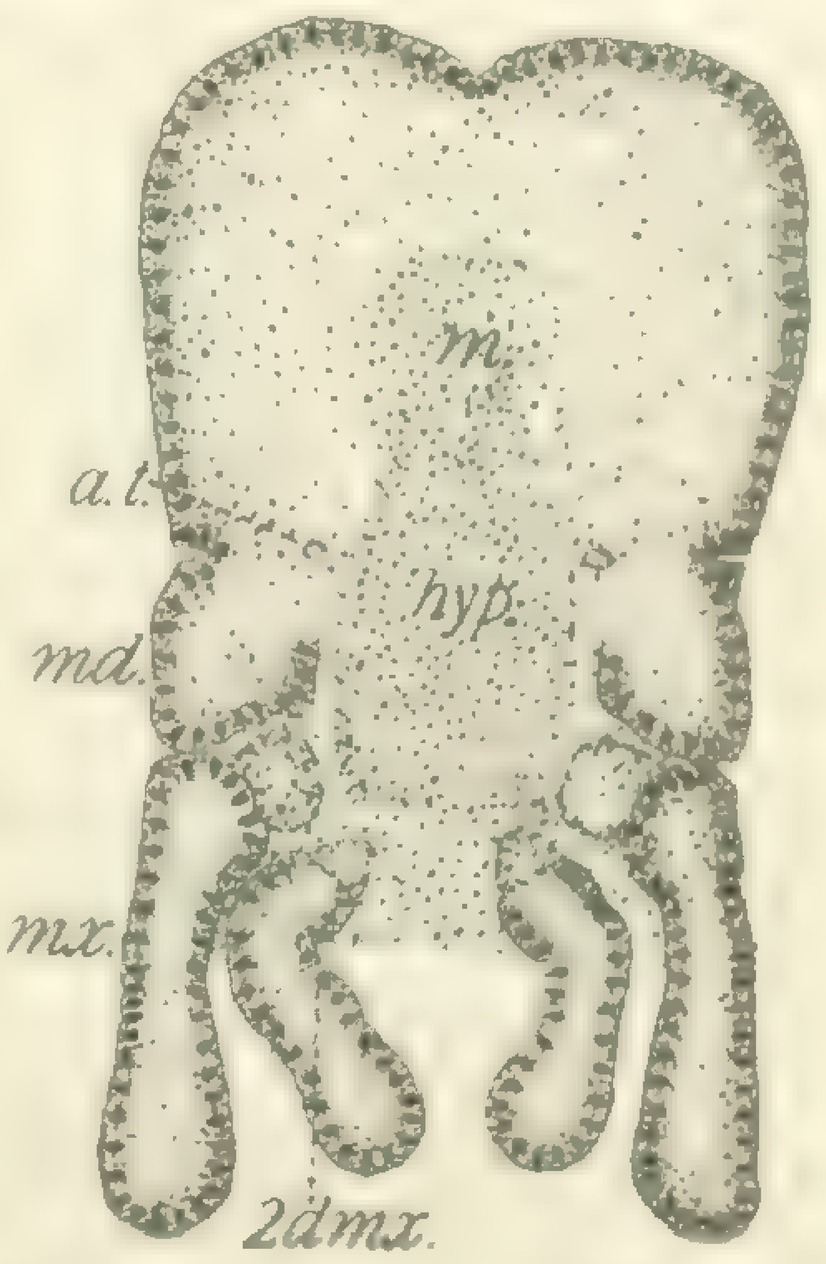

FIG. 12.—Ventral view of embryo of sixteen days. The antennæ and the procephalon have been removed to expose the hypopharynx. × 80.

The procephalon is much enlarged and at its proximal end is wedged in between the cephalic lobes in the manner described by Huxley ('58).

The change which Weismann described as a rotation of the cephalic lobes as upon an axis, occurs during the latter part of the sixteenth and the early part of the seventeenth days. This change is best followed by observing the relations of the brain lobes and of the tendon invaginations to the rest of the cephalic region. At its close the cephalic lobes have pushed over the mandibles in such a way as to crowd back the mandibular pleurites. The mouth parts assume much their definitive position, and the head is practically formed, though it is not until much later that the sclerites have become so chitinized as to be perfectly distinct.

The Development of the Tentorium.

The tentorium or internal skeleton of the head of the adult cockroach has been described and figured by Miall and Denny ('86) and, more fully, by Comstock and Kochi (:02). The latter have treated of its structure in a number of forms, and have shown that its attachments afford valuable criteria for homologizing sclerites in different insects.

In the adult Blatta the body of the tentorium consists of a

chitinous plate underlying the œsophagus and protecting the sub-œsophageal ganglion. From the anterior margin of the body of the tentorium there extends forward a pair of processes, the *anterior arms*, which are attached at the cephalo-lateral angles of the clypeus, near the bases of the mandibles. Corresponding with these are the *posterior arms*, which are near the margin of the occipital foramen, just above the articulation of the maxillæ. In addition there passes up from the body of the tentorium to be inserted at the margins of the antennal sclerites, a third pair of processes, the *dorsal arms*. The entire structure arises from two pairs of ectodermal invaginations.

As early as the thirteenth day there appears cephalo-mesad of the base of the mandibles a prominent pair of invaginations which give rise to the anterior arms (Fig. 9, *a. t.*). These invaginations lie close to the latero-anterior angles of the mandibular ganglion. Heymons refers to the anterior arms in Forficula as originating at the base of the antennæ. In Blatta they are hidden by the antennæ, which must be removed in order to see the invaginations distinctly; but they clearly belong to the mandibular segment.

The invaginations for the posterior arms lie cephalo-laterad of the bases of the 2nd maxillæ (Fig. 10, *p. t.*) They are much less prominent than those of the anterior arms, and, more or less hidden by the 1st maxillæ, they are difficult to detect. They seem to be somewhat retarded in their development, for I have been unable to find them in embryos which clearly showed the invaginations in the mandibular segment.

The invaginations of the anterior arms extend upwards along the sides of the mandibular ganglion, and then, bending at an angle, pass caudo-mesad. At a comparatively late date the two invaginations fuse, and thus give rise to the main body of the tentorium. On the other hand the posterior invaginations pass as blind sacs slightly upward and then forward, to fuse ultimately with the anterior arms.

While the anterior and the posterior arms thus originate as invaginations of the body-wall, the dorsal arms arise, not as invaginations but as processes, from the anterior arms. These processes gradually extend dorsad and thus come into connec-

tion with the body-wall in the region of the antennal sclerites. Figure 11 shows diagrammatically the course of the tentorial arms in an embryo of about eighteen days.

Considering the rapid growth of the embryo during the period following their appearance, the development of these rudiments is but slow. It is not until the twentieth day or later that the fusion of the two pairs of rudiments has taken place.

In view of this method of origin of the dorsal arms of the tentorium of Blatta, it is interesting to note the condition in the Plecoptera, a group in many respects more generalized than the Blattidæ. Of the dorsal arms in these forms Comstock and Kochi, p. 41, say: "In the Plecoptera it appears to be merely a chitinized tendon, the peripheral end of which is less chitinized than the base and is only loosely attached to the skull." Believing that in other insects the anterior arms arise from a distinct invagination, these authors continue: "It remains to be determined whether or not the dorsal arms in the Plecoptera are homologous with the apodeme-like dorsal arms in other insects and, if so, which type is the more generalized." As has been seen, the evidence of embryology shows that the generalized condition is that which still persists in the Plecoptera.

The most thorough study of the development of the tentorium was that of Heider ('89). In addition to this investigator, several others have devoted more or less attention to the subject. Hatschek ('77) called attention to what he supposed were tracheal invaginations in the head of lepidopterous embryos. Tichomiroff ('79) says: "There exists no head tracheæ such as Hatschek thought he discovered. The epithelial invaginations here found I believe to be the rudiments of the inner head-skeleton." Ayers ('84) noticed invaginations in the head region, but was unable to determine their rôle. He inclined to the belief that they disappear altogether, "as no trace of them was to be found in sections of an embryo about the time of hatching." Wheeler ('89) attributed the tentorium to five pairs of invaginations anterior to the maxillary segment.

My results agree with those of Heider, who described the tentorium as arising from two pairs of invaginations, one in the

mandibular and one in the second maxillary segments. Heymons ('95) basing his conclusions mainly on a study of Forficula, described essentially the same conditions, as applying to Forficula and to the Orthoptera, including the Blattidæ. Carrière and Bürger made the same observations on Chalicodoma, thus lending strength to Heymon's surmise that such a mode of origin is typical for the entire group of insects.

Various investigators, among whom are Palmen ('77), Hatschek ('77), Wheeler ('89), and especially Carrière ('90), and Bürger ('97), have regarded the tentorial invaginations as homodynamous with the tracheal invaginations. To this Korschelt and Heider ('93) object that their rudiments do not by any means everywhere agree so closely with tracheal stigmata of the following segments as they do in Chalicodoma. This is especially true of these rudiments in Blatta. As we have seen, the invaginations for the anterior arms arise close to the median line, just laterad of the nerve cord. This corresponds more nearly to the position of the invaginations for the thoracic furca. The origin of the posterior invaginations is more suggestive of the stigmatic invaginations.

In considering this question it must be remembered that Chalicodoma is a highly specialized type with an interpolated larval stage, while Blatta is a representative of a comparatively generalized group of hemimetabolous insects. This being the case, it does not seem that we should regard the location of the tentorial rudiments in Chalicodoma as primitive, but rather I should regard it as secondary. The fact urged by Palman, that the chitinous lining of the tentorium, like that of the tracheæ, is shed during ecdysis, is of little weight, since the same holds true of any hollow ectodermal invagination in insects.

However, it is not necessary to conclude that the tentorial invaginations are metamorphosed tracheæ "which have lost their primitive function and become secondarily modified." If, with Kennel, we derive the tracheæ from dermal glands of annelidan ancestors, there is no reason why we should not consider the tracheæ and the tentorium as homologous structures. Certain of these glands definitely localized have become modified to form tracheæ, while certain others, of the same origin though not

homodynamous with the first, have become converted into the tentorium.

The Development of the Head Sclerites.

As before stated, it is only in the most incidental manner that insect embryologists have touched upon the development of the head sclerites. Before presenting my conclusions concerning the development of the head capsule of Blatta, I shall briefly review the more important of the scattered references, reserving comment until we are ready to compare the views thus expressed with the results of my work.

The earliest of the references was that of Zaddach ('54). This pioneer worker has not received due credit for what he so independently accomplished. Many general features of the embryological development of insects, though credited to much later writers, were clearly outlined by Zaddach. Working altogether with entire mounts, it is but natural that his conclusions regarding the external changes should be the most accurate. It was he who first pointed out the post-oral origin of the antennæ, and called attention to a special antennal segment distinct from the cephalic lobes. He described the procephalon ("*Vorderkopf*"), and derived from it the labrum, the clypeus and the front ("*hinterer und vorderer Kopfschild und Oberlippe*"). He believed that the cephalic lobes formed the bulk of the head capsule, while the Y-shaped suture represented the line of fusion of the cephalic lobes and the procephalon.

Huxley ('58) gave a more accurate description of the procephalon. He also gave a fuller account of the dorsal flexure of the cephalic region, as a consequence of which "the line of attachment of the bases of the eyes and antennæ is frequently altogether above that of the other appendages, so that they appear to be tergal, and not sternal, appendages." The procephalic lobes he regarded as the sternite of the first, or opthalmic, segment and though he does not make a direct statement, the inference is that his "antennulary and antennary sterna" are represented by the labrum and the clypeus.

Packard in his earlier work devoted some attention to the

study of the development of the head sclerites. In 1866 he argued that "since the arthropleural is the limb-bearing region of the thorax it must follow that this region is largely developed in the head," the sternites being reduced to a minimum and the tergites almost completely absorbed. He believed that the bulk of the head is formed "by the great expansions of the eye-pleurites which, so to speak, are drawn back like a hood over the basal rings."

In 1870, in the second edition of his "Guide to the Study of Insects (foot-note)," he reiterates these conclusions. He distinguishes the labrum, epipharynx, and clypeus as tergal elements belonging to his hypothetical pre-ocellary segment. The occiput also is reckoned with the tergites, while the gula is sternal. All of the other elements of the capsule are supposed to be pleural.

Packard later completely revised his views as to the number of primitive head segments. Instead of seven or a possible eight, he recognized but four segments entering into the formation of this region. In 1883, in his paper on "The Number of Segments in the Head of Winged Insects," he thus summarizes his views as to the development of the sclerites:

"It appears, then, that the epicranium or that piece (sclerite) bearing the eyes, ocelli, and antennæ, and in front of the clypeus and labrum, is formed from the original procephalic lobes, and represents the first or antennal segment; while the remainder of the original or primitive segments are obsolete, except in those insects which retain traces of an occiput or fourth cephalic tergite. All of the gular region of the head probably represents the base of the primitive second maxillæ."

Ayers ('83) refers to the reduction of the maxillary and mandibular segments, "their dorsal portions disappearing altogether and their ventral portions fusing with the oral region."

Viallanes ('86 and '87b) states that the head of an insect presents three prebuccal segments and that the labrum represents the sternite of the third or tritocerebral segment. Beyond this he does not enter upon a discussion of the origin of the sclerites.

Heider ('89) was the first to devote especial attention to the development of the tentorium. His careful studies of the origin

of this structure have already been discussed. Regarding the sclerites he states that the labrum and the clypeus arise from the procephalon, while the remainder of the head capsule is formed mainly by the bending over dorsally and the backward extension of the cephalic lobes.

It is Heymons who has devoted the most attention to a study of the embryological development of the head sclerites. Studying mainly the development of various species of the Orthoptera, he very definitely stated his conclusions in his paper on the segmentation of the insect body ('95a). The labrum and the clypeus he derives from the procephalon, while the front, he concludes, is developed from the fused cephalic lobes. The vertex, occiput and genæ he believes are developed from the fused tergites of the mouth part segments, while the hypopharynx arises from the fusion of the sternites of these same three segments.

Janet, '99, finds in the sclerites but little indication of the primitive segments. Thus he finds that the front "appartient, par sa partie antérieure, au somite clypéopharyngien; par sa partie postérieure, au somite du labre; par ses parties latérales, au somite antennaire." Based upon years of study of the morphology of certain Hymenoptera, Janet's paper presents a fund of valuable anatomical data. From the embryological view point it is less satisfactory. Moreover, though recognizing the confusion in the use of terms to designate the head sclerites, Janet has made no attempt to determine homologies. Until this has been carefully done, results obtained from a study of such a group as the Formicoidea can be of but little general application.

On the other hand, Comstock and Kochi, :02, attach very great importance to the relation of the primary segmentation to the sclerites of the adult insect. Their conclusions were based upon comparative anatomical studies of a large series of the more generalized insects, as well as upon embryological data. According to their view, the typical segment is composed of two subsegments. Ventrally the line of union of these subsegments is determined by the position of the furcæ, while laterally it is similarly marked by the position of the lateral apodemes. Between the segments lie the tracheal invaginations, which these

authors regard as homodynamous with the invaginations of the lateral apodemes. Thus to these invaginations of the body wall is ascribed a prime importance in determining the homologies of the sclerites. Another valuable criterion they found in the relations of the appendages to a typical segment.

In addition to limiting and carefully defining the sclerites already generally recognized, Comstock and Kochi also distinguished four pairs of sclerites which had previously escaped attention. These were: 1st, the antennal sclerites bearing the antennæ; 2nd, the antecoxal pieces of the mandibles, a pair of sclerites in some species distinct from the clypeus and forming the ventral articulations of the mandibles; 3rd and 4th, two pairs of maxillary pleurites, narrow, chitinized bands between which articulate the cardines of the maxillæ. In addition to these four pairs of sclerites proper, there are two pairs which may have originally represented segments of appendages. These are: 1st, the ocular sclerites, a pair of annular sclerites bearing the compound eyes, and 2nd, the trochantins of the mandibles, a pair of sclerites between the mandibles and the genæ.

Their conclusions regarding the relations of the head sclerites to the primitive segments and to the appendages were summarized by Comstock and Kochi in the following table:

SEGMENTS	SCLERITES	APPENDAGES
1. Ocular (Protocerebral)	vertex and genæ .... front	Ocular sclerites
2. Antennal (Deutocerebral)	Antennal sclerites .... Clypeus proper	Antennæ
3. 2nd Antennal (Tritocerebral)	Labrum (mouth)	2nd Antennæ of Campodea et al.
4. Mandibular	Postgenae. .... Antecoxal pieces Pharyngral sclerites	Mandibles Trochantin

5. Superlingual		Superlingual
6. Maxillary	Maxillary pleurites Lingua	Maxillæ
7. Labial	Lateral cervical sclerites Dorsal cervical sclerites .... Vent. cerv. scl. (gula)	Labium

In each section of the middle column the dotted line indicates the division between the sternal and the lateral elements of the segment.

My results have convinced me that so intimate a relation between primary segmentation and the sclerites cannot be shown.

I find that the front, clypeus, and the labrum are all derived from the procephalon. This is in agreement with the conclusion of Zaddach, '54, whose "hinterer Kopfschild" is clearly the *clypeus posterior* of Newport or the *front* as defined by Comstock and Kochi.

Aside from Zaddach practically all authors agree in stating that from the procephalon arise the clypeus and the labrum. It has been suggested by Comstock and Kochi that the term *clypeus* has thus been used in a broad sense to include both the clypeus anterior and the clypeus posterior or the front.

That Heider used the word clypeus in a yet looser sense is evident. He speaks of the procephalon as giving rise to the clypeus and the labrum. Now, in Hydrophilus, the form upon which he worked, as well as in any of the Hydrophili, the larva does not possess a labrum (Schiodte, '61), or, more correctly speaking, the clypeus and labrum have fused without leaving any line of demarcation between them. Thus Heider has homologized the clypeo-labral sclerite as labrum only, while the front he has mistaken for the entire clypeus.

On the other hand, Heymons, as is shown by his figures, has correctly distinguished the front. Yet he states that the clypeus and labrum arise from the procephalon, while the front is formed from the fused cephalic lobes. He presents no evi-

dence, nor have I been able to find any in support of this view. There remains a consideration of the relation of these sclerites to the primitive segmentation. I have called attention to the fact that though Huxley, '58, does not make any definite statement to that effect, the inference is strong that he regarded these sclerites as representing the sternites of three preoral segments. In fact, in referring to the Crustacea, he says that the labrum represents the sternite of the antennary or third somite. Viallanes, who likewise refers the labrum to the sternite of his tritocerebral or third somite, seems to have attributed to these sclerites a similar definite relation to the primary segmentation.

More recently Comstock and Kochi have independently arrived at and very definitely present the view that the front, clypeus, and labrum represent respectively the sternites of the first three segments. In support of this view they lay much weight on Viallane's statement that the labrum is innervated by the tritocerebrum. Since the front bears one or more of the ocelli, it is obviously derived from the first or ocular segment. The intermediate sclerite, or clypeus, would then belong to the second segment. These writers also believe that the position of the antennal rudiments is only apparently post-oral, — that in reality the basal part of the antennal sclerites abuts against the procephalon.

The embryological evidence, however, shows that the procephalon, and thus the sclerites derived from it, — the front, the clypeus and the labrum, — belong to a single segment, the ocular or protocerebral.

I have discussed elsewhere the question of the primitive position of the antennæ, and have shown that in Blatta their rudiments are clearly post-oral at first.

Even if we were to grant that the antennal rudiments are only apparently post-oral, there can be no question as to the primitive location of the second antennæ and the third somite. Yet the hypothesis derives the labrum from the sternite of this segment.

While I should attach great value to the innervation as a criterion for determining the relation of sclerites to segments, I

do not believe that it can be regarded as absolute. At any rate, the evidence against the labrum as the sternite of the third segment completely outweighs this consideration.[1]

The procephalon develops entirely in front of the stomodæal invagination, and is already well outlined before the deutocerebral and tritocerebral ganglia have moved forward. Moreover, as Prof. Comstock suggested, the labrum and the clypeus give no satisfactory evidence of a paired origin. The absence of median sutures in these sclerites might be readily explained by the statement that fusion had taken place at such an early stage as to be complete. But a more serious objection is that if they develop post-orally and migrate to their pre-oral position, there should be a stage in which they are paired. Such a stage does not occur.

In the Orthoptera and in the Pterygota generally, the second antennal segment is so slightly developed and so transient as to have been largely overlooked by investigators, yet in these forms the labrum is usually strongly developed. On the other hand, in the Apterygota, where the second antennal segment is especially well developed, the labrum is comparatively insignificant.

Finally, the sutures separating the front, clypeus, and labrum are developed at a comparatively late period in the development of the procephalon. If these sclerites represented primary segments, we should find them developing from three distinct centers. The fact that the procephalon develops as a single piece shows that the sclerites derived from it are not primary, but are secondarily developed. In fact, they are not constant, but there are many species in which one or more of the sutures is lacking, and thus the number of sclerites reduced.

The vertex, the compound eyes, and with them the ocular sclerites and the genæ, are formed from the fused cephalic lobes and thus, with the front, clypeus and labrum, belong to the ocular or protocerebral segment. The median suture of the epicranium represents the ventral line of fusion of these lobes.

[1] It should be noted that Janet ('99) considers the labral nerves as in reality arising from the protocerebrum. This is more in harmony with the embryological evidence.

The V-shaped epicranial suture in Blatta separates the front from the vertex. It thus represents the line of separation between the cephalic lobes and the procephalon.

Heymons maintains that the front alone is derived from the fused cephalic lobes. The relatively excessive development of these lobes would indicate that they must enter more largely into the structure of the head. More weighty evidence is the fact that the front is separated from the compound eyes by the V-shaped suture. There is, of course, no question that the eyes belong to the first segment and are developed from the cephalic lobes. Moreover, in following through a series of embryos we can trace the manner in which the front develops by the extension of the procephalon into the angle between the fusing lobes. Thus the direction of this suture — an inverted V with the apex continuous with the median suture of the epicranium — is easily explained. Heymons emphasizes his belief that the suture represents the line of separation between the first and second segments. But if that were the case the rounded caudal margins of the cephalic lobes would on fusing present a V-shaped angle whose apex would be directed cephalad rather than caudad, as is really the case.

On first sight it would seem obvious that the genæ belonged to the mandibular segment. Huxley ('78) described the mandibles as articulating with this sclerite. To this, Miall and Denny ('86) take exception. Comstock and Kochi also call attention to the fact that the chief articulation of the mandibles is with the postgenæ rather than with the genæ. In the earlier stages, after the mandibles have moved forward, it appears as though the mandibular pleurites occupied the position of the future genæ. At the time of the rotation of the embryo, however, the cephalic lobes crowd forward over the dorsal end of the mandibular segment, and thus the pleurites are pushed back to occupy the position of the postgenæ.

It is easy to see how, as a result of this process of displacement of the mandibular segment, there should remain a portion to serve as the ventral articulation of the mandible. In the adult Blatta the limits of this remnant are not to be distinguished from the clypeus; but, as pointed out by Comstock and

Kochi, in Gryllus and in Corydalis there persists a definite sclerite. These authors have shown that this sclerite bears the same relation to the articulation of the mandible as does the antecoxal piece to the coxa of a thoracic leg, and they have therefore called it the *antecoxal piece* of the mandible.

Along the caudal margin of the postgenæ, but cephalad of the invagination for the posterior arm of the tentorium, is a narrow sclerite, which was first pointed out by Comstock and Kochi. Believing that the posterior tentorial invagination belonged to the first maxillary segment and was homodynamous with the invaginations of the thoracic lateral apodemes, these writers named this sclerite the *anterior maxillary pleurite.* A similar narrow sclerite lying parallel with the first, but caudad of the tentorial invagination, they called the *posterior maxillary pleurite.* We have seen that the posterior arm of the tentorium belongs to the labial segment. The position of its opening in the adult insect — almost directly over the cardo of the first maxilla — is due to the cephalo-mesal growth of the paired labial rudiment, as well as to the backward pushing of the maxillæ at the time of rotation. Thus the sclerite lying caudad of this opening belongs, not to the maxillary but to the labial segment, and should be known as the *labial pleurite.* The sclerite lying cephalad of the opening may retain the name of maxillary pleurite.

However, we cannot restrict the maxillary pleurite entirely to this narrow sclerite. There early takes place a fusion of the pleurites of the mouth part region. The position of the posterior tentorial invaginations serves to mark the anterior limits of the labial pleurite, but the extent of the mandibular and the maxillary pleurites can only be judged from the relations of their appendages. In an embryo of about the sixteenth day, as may be seen from Figure 10, the maxillary pleurites exceed in size either of the others. Though the rotation of the embryo results in a displacement of the maxillæ, I do not believe that their pleurites become reduced to the narrow, imperfectly demarcated sclerites which have been designated as the maxillary pleurites.

We have seen that a portion of the deutocerebral segment, bearing the antennæ, is more or less clearly marked off from the remainder of the germ band, even in the earlier stages. I

believe that this persists as the antennal sclerite of Comstock and Kochi. In embryos about ready to emerge these annular sclerites are very clearly marked, and allow of no question as to their equivalence to other sclerites.

There has been much discussion as to the origin and significance of the hypopharynx, though the data have been drawn almost solely from a study of comparative anatomy. Apparently the majority of those who have thus studied it regard it as representing a fused pair of appendages. Vayssiere ('82) who worked upon larval Ephemeridæ, strongly favored this view, though he adds that in order to settle the question studies of a number of representatives of the various orders would be necessary.

Folsom (:00) derives the hypopharynx of Anurida from a median unpaired evagination between the first maxillæ, and two small papillæ between the mandibles. The first gives rise to the lingua, while from the latter are developed the superlinguæ. The superlinguæ Folsom regards as the appendages of a distinct segment, provided with a small ganglion. He brings forward much evidence from comparative anatomy to show that the hypopharynx of Anurida is typical of the Apterygota. Further than that, he attempts to apply the same interpretation to the Pterygota.

The only worker who has devoted any attention to the embryological development of the hypopharynx of the Ptergota is Heymons ('95a). This investigator reached the surprising conclusion that the hypopharynx represents the fused sternites of the mouth part segments. That this interpretation is essentially correct my studies have convinced me. However, I would not attribute to the labial sternite any part in this structure. I believe that the hypopharynx of Blatta represents the fused sternites of the mandibular and first maxillary segments (Fig. 12, *hyp.*), and that of a consequence of the forward migration of the mouth parts these fused sternites have been pushed to within the mouth cavity.

In Blatta, then, the sternite of the labial segment is represented only by the ventral cervical sclerites. It seems to me very clear that Comstock and Kochi are right in regarding the gula of Coleoptera and certain other insects as representing the fused cervical sclerites.

My views in regard to the relations of the sclerites of the adult Blatta to the primitive segments may be summed up in the following table:

Segment	Sclerites
Protocerebral	Vertex, genæ. Front, clypeus and labrum.
Deutocerebral	Antennal sclerites
Tritocerebral	———
Mandibular	Part of post-genæ, trochantins Part of hypopharynx
Maxillary	Remainder of post-genæ, maxillary pleurites Remainder of hypopharynx
Labial	Labial pleurites; lateral cervical sclerites Ventral cervical sclerites

From the above results it would seem that the definitive sclerites can afford us little or no evidence as to the primary segmentation of the insects. This is certainly true of the head sclerites, and I see no reason why it should not apply to other regions of the body. Sclerites originate from mechanical causes, and do not necessarily have any relation to the primary segmentation.

As an illustration might be cited the breaking up of the annular segment into sternite, pleurites and tergite. The circumcrescence of yolk and the consequent formation of the lateral and dorsal portions of the embryo is a process of gradual growth, and there is no demarcation into separate areas. The distinction into sternite, pleurites, and tergite is a secondary process.

More germane is the fact of the origin of the front, clypeus, and labrum from the procephalon. Thus not only these three sclerites but also the vertex and the genæ arise from the one segment, the protocerebral. I have shown, also, that the post-genæ are to be regarded, not as the pleurites of a single segment, but as the fused pleurites of the mandibular and maxillary segments.

I would not depreciate the value of the sclerites as an index to relationship among insects. That they are to a marked

degree constant, and that they may be homologized in the different groups, I believe to be very true. That they are secondary is equally true, and thus evidence drawn from a study of the sclerites of the adult insect is insufficient to determine the primitive segmentation and the related question as to the compound nature of the segments.

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THE ARBOREAL ANCESTRY OF THE MAMMALIA.

W. D. MATTHEW.

WITHIN the last few years Dollo and Bensley have adduced strong arguments to show that the marsupials are descended from arboreal ancestors, as indicated especially by the traces in modern marsupials of former opposability in the first digit of the manus and pes.[1] The present writer has for some time been of the opinion that this is true not only of marsupials, but of the placentals as well. Our present knowledge of fossil Mammalia and of the course of evolution of the various modern races, enables us to foreshadow with considerable detail the characters of a common ancestral group (homogeneous in adaptive characters, although perhaps embracing certain differences in dentition etc., of very ancient origin) from which all known mammals, excepting the Prototheria, are descended. That there was such a group ancestral to both metatherian and eutherian mammals is, I believe, reasonably certain. The evidence for it is the close uniformity of these Mammalia in general structure in spite of their wide divergence in adaptive specialization, and the invariable approximation towards a central type of each race whose development is known from palaeontology. As a preliminary to further discussion we may point out the characters of this primitive central type.

1.—*Size very small, skull of moderate length, brain case completely enclosed in bone, brain of high type compared with that of reptilia although lower than in the modern mammals.* In every case where we are able to trace the descent of the large modern mammals, we find their direct ancestors successively smaller as we pass backward in time. The horse and camel have been traced back nearly to the beginning of the Tertiary; their ear-

[1] This view was expressed by Huxley in 1880.

liest representatives are no larger than rabbits. Elephants, rhinoceroses, tapirs, every race about whose ancestry anything is known, exhibit a reduction in size corresponding to the distance back through which we have been able to trace them. The large animals of the early Tertiary are in every case early specializations which have left no descendants.

2.—*Molar teeth* "*bunodont*" i. e., *low crowned, the crowns composed of a few low broad rounded cones, heavily enamel-covered. The molars are tubercular* (*crushing*) *teeth, the premolars trenchant* (*cutting*), *the canines moderately large* (*piercing*), *the incisors small spatulate* (*nipping*) *teeth. The teeth were arranged in continuous series, except for slight gaps behind the canines.* The labors of Cope, Osborn and many other palæontologists have amply demonstrated this as the primitive type of dentition among the Mammalia. Whether we accept the whole of the Tritubercular Theory or not, this part of it appears to be beyond question.

3.—*Neck rather short, slender and flexible, permitting quick and easy turning of the head in all directions. Trunk slender, flexible, ribs rather short and few in number, lumbar region long and comparatively flexible.* These features characterize all early Tertiary mammals, without exception.

4.—*Tail very long and flexible, with strong muscles towards the base, and probably prehensible.* All primitive Tertiary mammals have remarkably long and strong tails. These differ from those of the cats and resemble those of the prehensile-tailed monkeys in the greater breadth of the zygapophyses of the proximal caudal vertebrae and great size and length of the median caudals.

5.—*Shoulder girdle of scapula and clavicle.* No indications of a separate coracoid have been observed in early Tertiary mammals, but the clavicle was certainly developed in the ancestors of several groups which do not now possess it, and was probably generally present in the earliest types.

6.—*Ilia narrow and rod-like*, gluteal muscles long and slender.

7.—*Upper members of limbs comparatively long and loosely jointed to the trunk, permitting great freedom of motion.* The

great relative length of the humerus and femur is a striking feature in the limbs of all early Tertiary mammals. In the evolution of the limbs for running the femur and humerus have generally been reduced in length and compacted into the flank, while the lower legs and feet are elongated. This places the heavy muscles high up on the limb, and by bringing its centre of gravity near to the proximal joint, enables it to swing more rapidly through a considerable arc. Thus the animal gains in length of stride without losing in quickness of step and can maintain a high speed for a long distance with less fatigue.

8.— *Ulna and radius separate, equal in size, radius with round head, permitting free supination and pronation. Tibia and fibula separate with probably more limited motion.*

9.— *Wrist and ankle very flexible, all the carpals separate and a centrale present. Astragalus with flat trochlea, distinct neck and rounded head.* This type of carpus and tarsus is found in all Basal Eocene mammals. It is retained with but little change in primates, insectivores, most rodents, and some other groups. Its gradual conversion into the various types seen in other groups is demonstrable in the Amblypoda, Condylarthra, Carnivora, partly so in the Proboscidea and Edentata, but not in the Artiodactyla and Perissodactyla which have already developed their peculiar types of astragali when they first appear in the geological record.

10.— *Five digits on each foot, the joints permitting of very free motion of fingers and toes, which were tipped by small claws.* The argument for the derivation of all mammals from pentadactyl ancestors has been fully set forth by Cope and others. The derivation of the hoofed from clawed types is likewise indicated in various lines of descent as now known.

11.— *First digit more or less opposable in both manus and pes.* This is contrary to the usual assumption that the opposable thumb found in several groups of arboreal mammals is in each case a new adaptation to their habits of life. But there is considerable evidence for it. In the first place, as far as we can trace back the history of each of the arboreal groups, we find their first ancestors with the first digit as fully opposable as in the modern representatives (*e. g.*, the Middle Eocene primate

Notharctus). Second, in those groups which have not an opposable thumb, we find as we trace back their ancestry that the trapezium, whose form and facets give the surest indication on this point, approaches more and more nearly to the type preserved in the Primates, etc. It becomes large, triangular, with very concave distal facet for the digit, and round-conical proximal faceted end abutting against the scaphoid, trapezoid and centrale. In the four Basal Eocene mammals (Pantolambda, Euprotogonia, Clænodon and Dissacus) in which this part of the skeleton is known, the form of the bone is surprisingly uniform, and when the manus is put together, the first digit is thrown partly outward from the rest of the hand, and permits of much freer motion than the remaining digits, with a considerable degree of opposition. With the development of the foot for terrestrial locomotion the trapezium and first metacarpal lose their mobility, the rounded conical proximal facet of the former separates into two flat facets at right angles for scaphoid and trapezoid, its distal facet becomes more plane and its whole distal end reduced in width and closely appressed against the proximal end of the second metacarpal, which it overlaps. In the further evolution of the running foot the first digit is reduced to a nodule and finally disappears, and the trapezium usually follows suit, the trapezoid either remaining separate (Perissodactyla) or being consolidated with the magnum (Artiodactyla).

The primitive opposability of the hallux is less clearly indicated, but the close resemblance in the form and arrangement of the internal tarsals, especially the internal cuneiform, in all early mammalia, to the intermediate stage in the evolution of the running carpus outlined above, very strongly suggests that the original condition in the tarsus was the same as in the carpus, but that its evolution for terrestrial locomotion began earlier or proceeded more rapidly.

In the third place, if we suppose, as many anatomists have done, that the so-called first metacarpal is really a proximal phalanx, and that the trapezium is the true first metacarpal, the hypothesis that all mammals passed through a stage when the pollex and hallux were opposable would supply a good reason

for the development of this anomaly, and would explain (*a*) the presence of but two phalanges on digit I, three on each of the others; (*b*) the epiphysis of digit I being proximal as in the phalanges, instead of distal as in the remaining metapodials; (*c*) the anomalous musculature of digit I on all mammals, the object of which is clearly seen when the digit is opposable, but is quite unexplained otherwise.

It would be beyond the purpose of this article to give at all fully the facts which support the above characterization of the primitive mammalia, but enough has been said to show the general nature and force of the evidence on which it is based. The modern orders of mammals have departed to a varying degree from this primitive type. The arboreal primates retain most nearly the primitive character, except that the limbs are elongated, the face is shortened and the brain greatly increased in size and complexity. The rodents, largely perhaps on account of their small size, have usually retained a great deal of the primitive skeleton character, but the dentition is much modified — least of all in the arboreal squirrels, which are almost unaltered in dental characters from the first known rodentia of the early Tertiary (Paramys, etc.). The Insectivora likewise retain many primitive characters, but in most cases in combination with one or another high specialization of an unusual kind. The Carnivora retain the primitive character more or less completely in the neck, trunk and legs, but show much greater adaptive changes in the feet and especially in the teeth. (Several of the Creödonta have a more or less opposable pollex, but this is lost in the later carnivora.) The Ungulata are by far the most highly altered group among the land mammals, almost every part of the body having gone through great adaptive changes, although the evolution is most marked in teeth and feet. We are able to trace the history of these changes more fully in this than in any other order, as its geological record is more complete. The Edentata early developed certain remarkable specializations which soon obscured their primitive characters. Of the remaining orders of placental mammals our geological record is very imperfect, and their relationship to the central type mainly hypothetical. The

marsupials, as Dollo and Bensley have shown,[1] are probably descended from an arboreal type which must have closely resembled the arboreal ancestors of the placentals, but with distinctions in the number and succession of the teeth, the origin of which is not yet clear. In these, as in the placental mammals, the modern arboreal forms are the most primitive. But it should be remembered that we know comparatively little about the palæontology of the marsupials earlier than the Quaternary, while we are able in most of the families of Ungulata, Carnivora, Rodentia and some other orders of placentals, to trace back their ancestry into the Middle or Lower Tertiary, and find them in every case converging toward the type characterized above, and quite closely converging as we come into the Basal Tertiary. We are thus enabled to place the earliest divergence from this central type in the Middle or Upper Cretaceous.

It may almost be taken for granted that if the characters of this central type were in all respects as stated above, it must have been of arboreal habitat. All its adaptations would be suitable for such a mode of life, and some would be more or less unsuitable for any other. The various modern groups (monkeys, squirrels, arboreal insectivores, opossums) which have retained this habitat are the least altered in structure, while the amount of structural change in other groups, as shown by their known palæontology, is proportioned to the change in their mode of life, the Ungulata exhibiting the greatest changes.

The hypothesis may be stated as follows:

The Cretaceous ancestors of the Tertiary mammals were small arboreal animals of very uniform skeletal characters, but probably somewhat differentiated in dentition according as fruit, seeds and nuts, or insects, formed the staple of their diet. At the beginning of the Mesozoic the available modes of life for land vertebrates were chiefly the amphibious-aquatic,

[1] A further development of the arboreal adaptation of the foot appears to have distinguished the marsupials, in the complete opposability of the hallux, with enlargement of the fourth digit and syndactyl reduction of digits II and III. It is this feature that is regarded by these authors as especially indicating arboreal habits.

the arboreal and the aerial, the terrestrial habitat being subordinate because the upland Flora was largely undeveloped or inedible as compared with its present condition. The three available provinces were occupied by reptiles, mammals and birds respectively. In the later Cretaceous the spread of a great and varied upland flora vastly extended the terrestrial province, and opened a new and constantly widening field for the expansion of the mammalia. These then commenced a great evolution, the new terrestrial groups expanding continually and becoming adapted to various modes of life. The arboreal types maintained or increased their lead in intelligence, but changed comparatively little in other respects. The terrestrial types became far more numerous and dominant, adapting their primitively arboreal organization to their various modes of life, yet retaining, in spite of extensive changes, a certain fixity of type which had been impressed upon them by their long arboreal residence.

The great extension of the terrestrial province in the Tertiary may be supposed to have opened a correspondingly large field for the expansion of the birds, but these, retaining in the main their aerial life, suffered but little change in organization, and the vast majority are today as homogeneous in skeleton structure as the mammals were at the beginning of the Tertiary. Coincident with the expansion of the terrestrial province was a great contraction of the amphibious-aquatic province. The extensive swamps and deltas and great inland seas of the Cretaceous, shrank at its close to small proportions, and the Reptilia underwent a corresponding diminution, some groups completely disappearing, others surviving through the Tertiary in continually decreasing numbers, the land reptiles (lizards and snakes) alone prospering. Both birds and reptiles, so far as they have retained their typical habitats, have changed but little structurally since the Mesozoic; only the few terrestrial reptiles and terrestrial or aquatic birds show an amount of change comparable with that in the terrestrial mammalia. It would seem therefore that all the facts accord with the explanation of the evolution of mammals during the Cenozoic as caused by their invasion of a new province and change of habitat from arboreal to dominantly terrestrial.

The little that is known of the Mesozoic Mammalia fits in with our hypothesis of their arboreal habitat but adds little to the evidence in its favor. Practically nothing is known of their skeletal structure; they are all of small or minute size, with teeth of insectivorous or granivorous type. They have been referred to monotremes, marsupials and insectivores, in each case on very insufficient evidence, but their ordinal relationships have little to do with the question of their habitat and need not be considered here. Their minute size, and association, in strata of fresh or brackish water origin, with large amphibious and aquatic reptiles and with abundance of fossil wood, suggest that the deposits in which they occur were laid down in extensive forest-clad river deltas and coastal swamps, and that the minute mammalia represent the arboreal fauna of these forests.

I am not well acquainted with the embryologic evidence which might bear upon the hypothesis advocated in this paper. Most investigations into mammalian ontogeny have had other problems in view. The deviation of placentals from marsupials or vice versa, and the ultimate origin of the mammalia from amphibian or reptilian ancestors, do not directly affect the question of the habitat of the Mesozoic ancestors of the Tertiary mammals. But undoubtedly important evidence on this point could be obtained from the ontogeny of their modern descendants, although not, perhaps, of the same force as the more direct evidence from palæontology.

American Museum of Natural History,
June 15th, 1904.

LOCALIZED STAGES IN COMMON ROADSIDE PLANTS.

JOSEPH A. CUSHMAN.

The plants considered in the present study are of common occurrence along country roadsides. With, perhaps, the exception of some of the early stages of development, the leaf forms noted may be found on country roads in the spring or summer. Although among our commonest plants, some actually classed as weeds, the stages shown in their development are as striking as could be found in any plants. The stages in development of other common plants have been described (*Amer. Nat.*, Vol. 36, No. 361), as well as some exotic plants of the Botanic Gardens of Harvard University (*idem.*, Vol. 37, No. 436). My thanks are due to Dr. R. T. Jackson for corrections and helpful suggestions. Each species is treated separately and its stages described in detail.

Thalictrum polygamum Muhl. Figures 1, 2.

(Tall Meadow Rue.)

Although this plant does not become conspicuous by its flowering until midsummer, its early growth from the rootstock and seedlings must be looked for in moist ground very early in the spring.

In the seedling (Fig. 1) the first nepionic leaf is simple, with three lobes Such a first leaf is frequently found, but fully as often the first leaf is like the second leaf in the figure. The second leaf is trifoliolate, each leaflet being like the whole of the first nepionic leaf as figured. From this point the leaves of the young plant, as added, increase in complexity, the plant finally producing the 2–3 ternately compound leaves characteristic of the adult.

As the plant is a perennial its early spring growth may be easily studied.

When first noted it usually has complicated leaves, but if the very earliest growth is looked for, leaves will be found exactly comparable to those of the seedling. The trifoliolate form is commonest, but in some cases, especially where the plants grow in sandy soil, the first leaf will be simple, as in the first leaf of the seedling. The steps in the further complication of the compound leaf follow the same stages as in the seedling, but usually more rapidly, arriving at the typical leaf of the species by fewer stages than in the seedling. This is a good example of acceleration of development seen in localized stages.

Fig. 1.—Seedling of *Thalictrum polygamum*, showing cotyledons, *c*, *c*, and first and second nepionic leaves, the first with 3, the second with 5 leaflets.

The plant produces great masses of the small flowers, and the strength thus used up is deducted from the amount which goes to leaf development, with the result that below the flower there is always shown localized senescence, exhibiting regressive development. Figure 2 shows leaves in the series below the flower panicles. There is a gradual reduction of the proximal portion as shown in leaves 1 and 2, until a leaf is produced (Leaf 3 of Fig. 2), in which the leaf is trifoliolate, as in leaf 2 of Figure 1, but having no lobes on the lateral leaflets. Next, the lobes of the terminal leaflet are reduced and the outline of all the individual leaflets thus becomes entire. Still later the two lateral leaflets disappear and a very small, simple, entire leaf is found (Leaves 5 and 6), simpler than anything seen in progressive development, either in the straight development of the seedling or the localized development in early spring

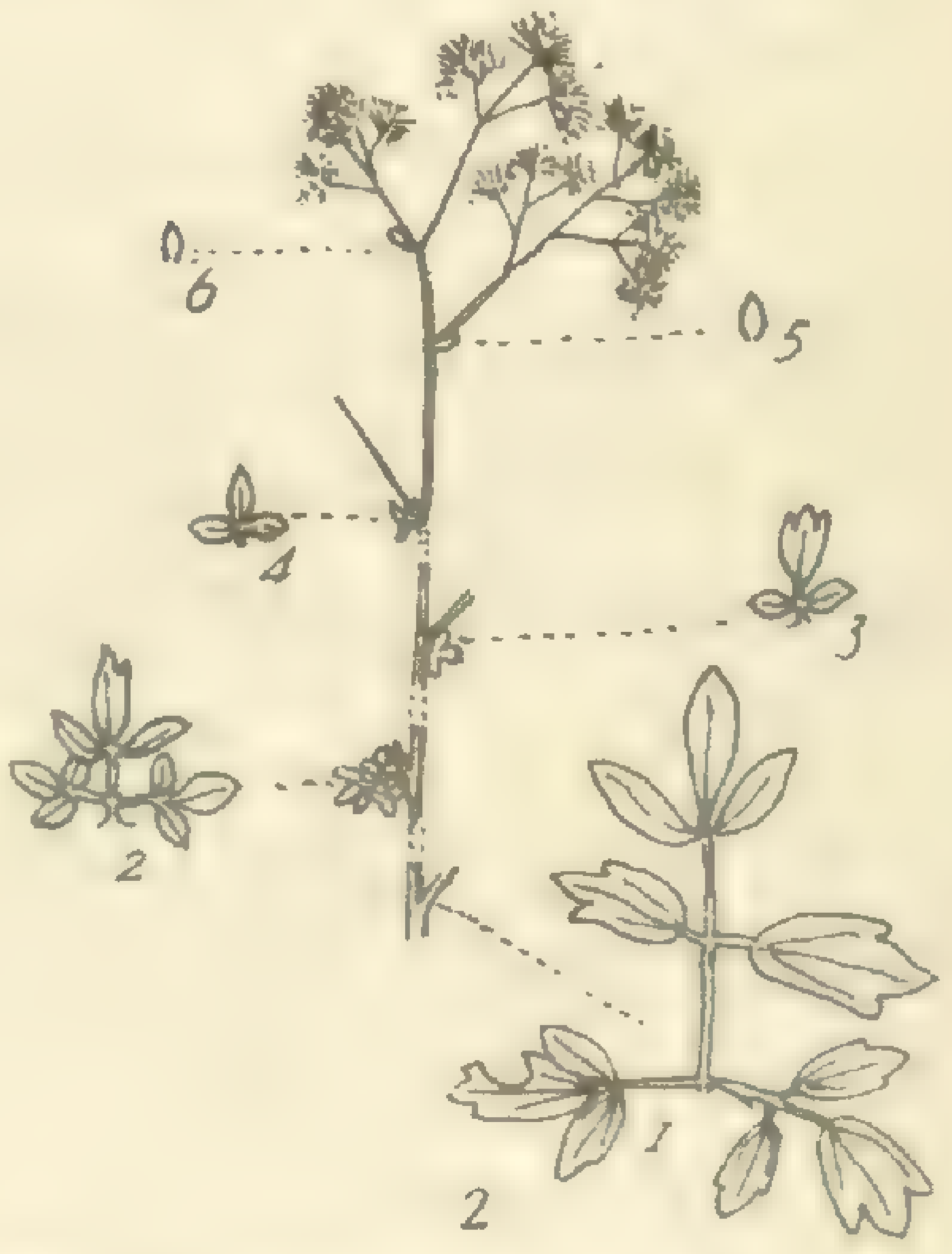


Fig. 2.—Flowering stalk of *Thalictrum polygamum* showing localized reversionary senescence below the flower. Leaves 1–6 enlarged to natural size.

growth. The stages below the flower are very noticeable and are easily made out.

Daucus carota L. Figures 3–13.

(Wild Carrot.)

In this common weed very marked localized stages are found. The direct development of the seedling shows much acceleration as the first leaf of the ordinary seedling is considerably complex. The first nepionic leaf of the seedling of this species is shown in Figure 3. It is a decidedly compound leaf. The second leaf is still more complex.

FIG. 3.—Seedling of *Daucus carota*, showing cotyledons, *c*, *c*, and first and second nepionic leaves.

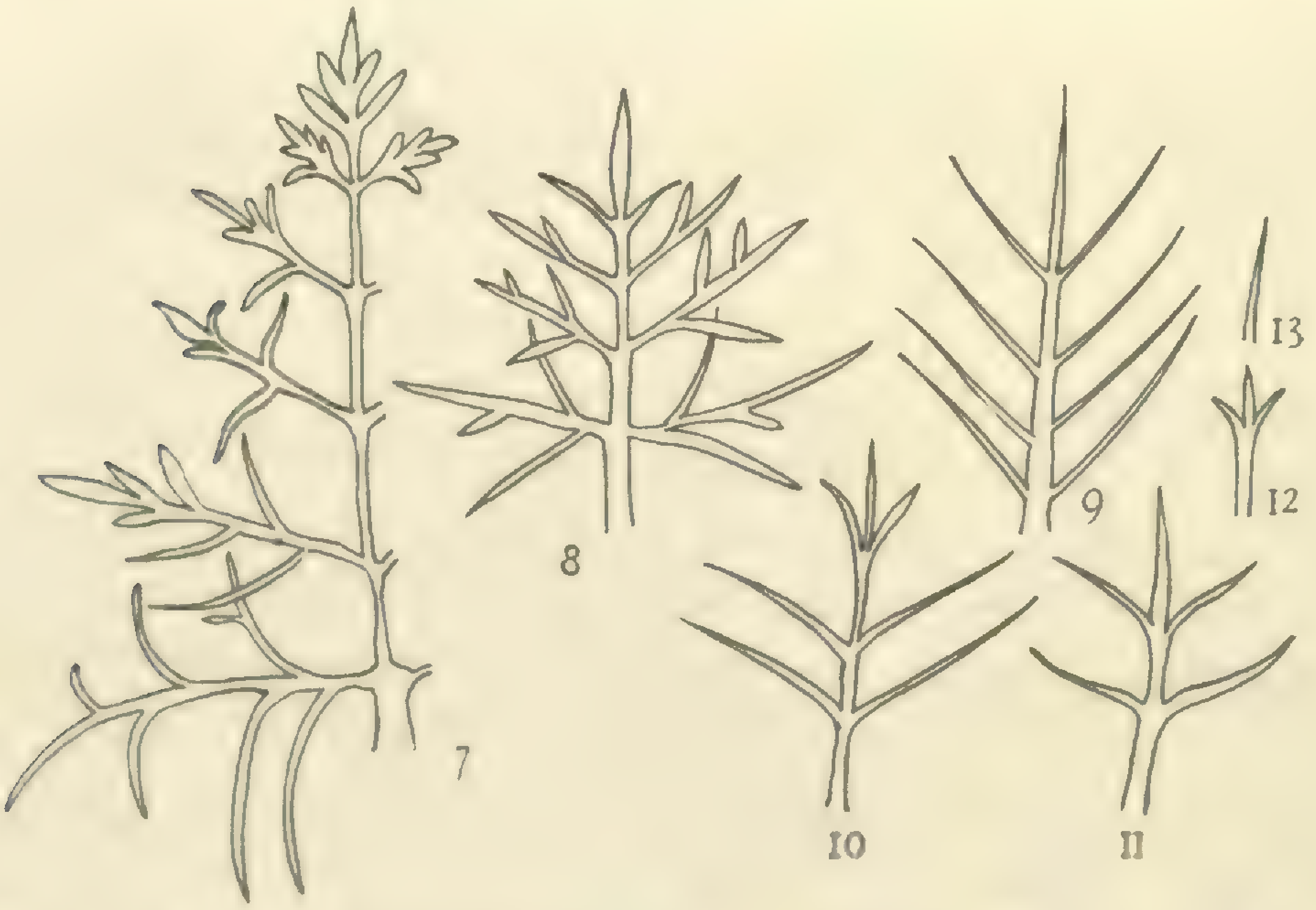
The spring growth is to some degree difficult of investigation, as the plant starts its growth very early. The first leaves seen under usual conditions of growth are very complex. It was therefore a matter of some trouble to obtain specimens showing reversionary characters. Finally plants growing under unfavorable conditions were sought. There the results were most gratifying. The plants shown in Figures 4–6 were found growing in sand along a railroad embankment where the conditions were decidedly adverse. They are of course weak specimens, although the size of the stem shows them to be adult plants of at least one year's growth.

FIGS. 4-6.—Spring growths of *Daucus carota*, 5-6 (1a-4a), weak growths; 4-6 (1-4), more vigorous growths.

In Figure 4, the first leaf of spring growth is simple and entire, the second leaf is similar but with a lobe on one side, the third leaf is trilobate and the fourth also. The fifth and sixth leaves have five lobes. In Figure 5, the stages except in the second leaf are exactly similar. From the plant

shown in Figure 6 two buds started. The series from the lateral weak bud, 1*a*–4*a*, are in the main like those of Figure 5, but the series from the stronger bud, 1–4, show a greater acceleration of development. The first leaf, No. 1, is comparable to the third leaf of Figures 4 and 5 and the third leaf of weaker growth on this same plant. The second leaf, No. 2, is comparable to the fifth leaf of Figure 4, and the third leaf is more complex than anything shown in the other cases of spring growth figured, but is closely comparable to the first nepionic leaf shown in the seedling (Fig. 3). In the localized development shown in early spring growth of weak plants, therefore, stages are found which are simpler than anything found in the direct development of the seedling. In vigorous plants spring growth is so much accelerated that these simpler stages are not found.

In Figures 7–13 are shown the leaves beneath the flower. Figure 7 shows the typical adult leaf of the stem, Figure 8 the upper leaf on the stem in the specimen examined. By comparing Figure 8 with the second nepionic leaf of the seedling (Fig. 3), it will be seen that the two are very similar except that the leaf tips are more acute, almost spiniform. Below the flower cluster there are what are usually termed "cleft involucral bracts." These



FIGS. 7–13. — Series of reduced leaves ("involucral bracts") found beneath the flower of *Daucus carota*, 7–8, upper leaves on the stalk; 10–13, clustered bracts beneath the flower, 13 being the upper one of the series.

are really reduced leaves as they are the morphological equivalent of such. Figure 10 is, in the number of its main division, comparable to the first nepionic leaf of the seedling (Fig. 3), and to leaf 3 of Figure 6 in the early spring growth. It differs however in not showing secondary lobes as seen in the other cases. Leaves of the next succeeding whorl have five main lobes, Figure 11, comparable to leaf 2 of Figure 6, or to leaf 5 of Figure 4. The one shown in Figure 12 is comparable to leaf 3 of Figure 4, or to the second stage in early spring growth. Figure 13 shows the ultimate reduction and a simple leaf comparable to the simplest first stage of spring growth. This series below the flower repeats in the reverse order, the steps shown in the progressive localized development of early spring growth and in the direct development of the seedling. In other words, it is regressive development repeating progressive development, but in the reverse order.

Baptisia tinctoria R. Br. Figures 14–16.

(Wild Indigo.)

This plant shows localized stages in a simple manner, yet very completely. In the direct development frequently starts off with the first nepionic leaf simple, broad and rotund, distally emarginate, the stipules not large but nevertheless noticeable (Fig. 14). The first leaf is broader and more rounded than the type leaf of the species (Leaf I of Fig. 16) in which the tip is slightly mucronate instead of slightly emarginate. The second nepionic leaf is trifoliolate, the leaflets rounded, wedge-obovate. The succeeding leaves are all trifoliolate, the stipules becoming smaller and less persistent.

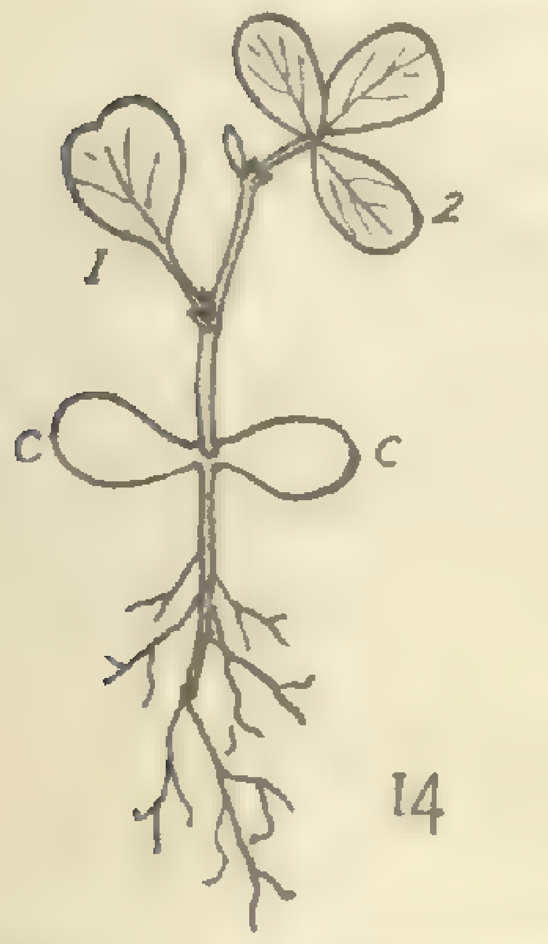


FIG. 14. — Seedling of *Baptisia tinctoria*, showing cotyledons, *c*, *c*, the first and second nepionic leaves, the first simple, the second trifoliolate.

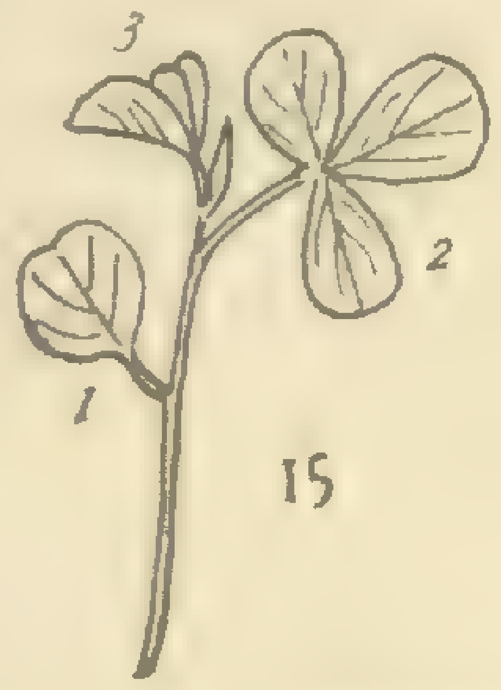


FIG. 15.–Early spring growth of *Baptisia tinctoria*, showing localized stages comparable to direct development seen in seedling.

Comparing these stages in direct development with localized stages in development seen in early spring growth,

the similarity is at once apparent. In some plants, probably but a year old, there were found many cases where the first leaf of spring growth was simple and emarginate, but like that of the first nepionic, much broader than the later leaves (Fig. 15). The stipules were also larger than in succeeding stages and in this again comparable to the first nepionic leaf of the seedling, showing a more accelerated condition. In all cases the second leaf of spring growth was trifoliolate. Those which were found with the spring growth starting off with a simple leaf were obtained in a situation unfavorable to the plant and thus favoring such retarded conditions of growth. The overlying loam had been removed from a glacial sand plain, leaving the sand exposed on a south slope. This gave a poor supply of moisture and exposed the plants to the full force of the sun. As a result, the plants showed a retarded development.

16

Fig. 16. — Flowering stalk of *Baptisia tinctoria*, showing the reduction of characters in the localized senescence below the flower.

In the adult plants, when in flower, cases of localized senescence are not infrequent. Below the flowers, the last leaf is often simple, comparable to the first nepionic leaf of the seedling (Fig. 14), and to the first leaf of spring growth in feeble or retarded plants (Fig. 15). This reversionary condition below the flower is not usually shown, however.

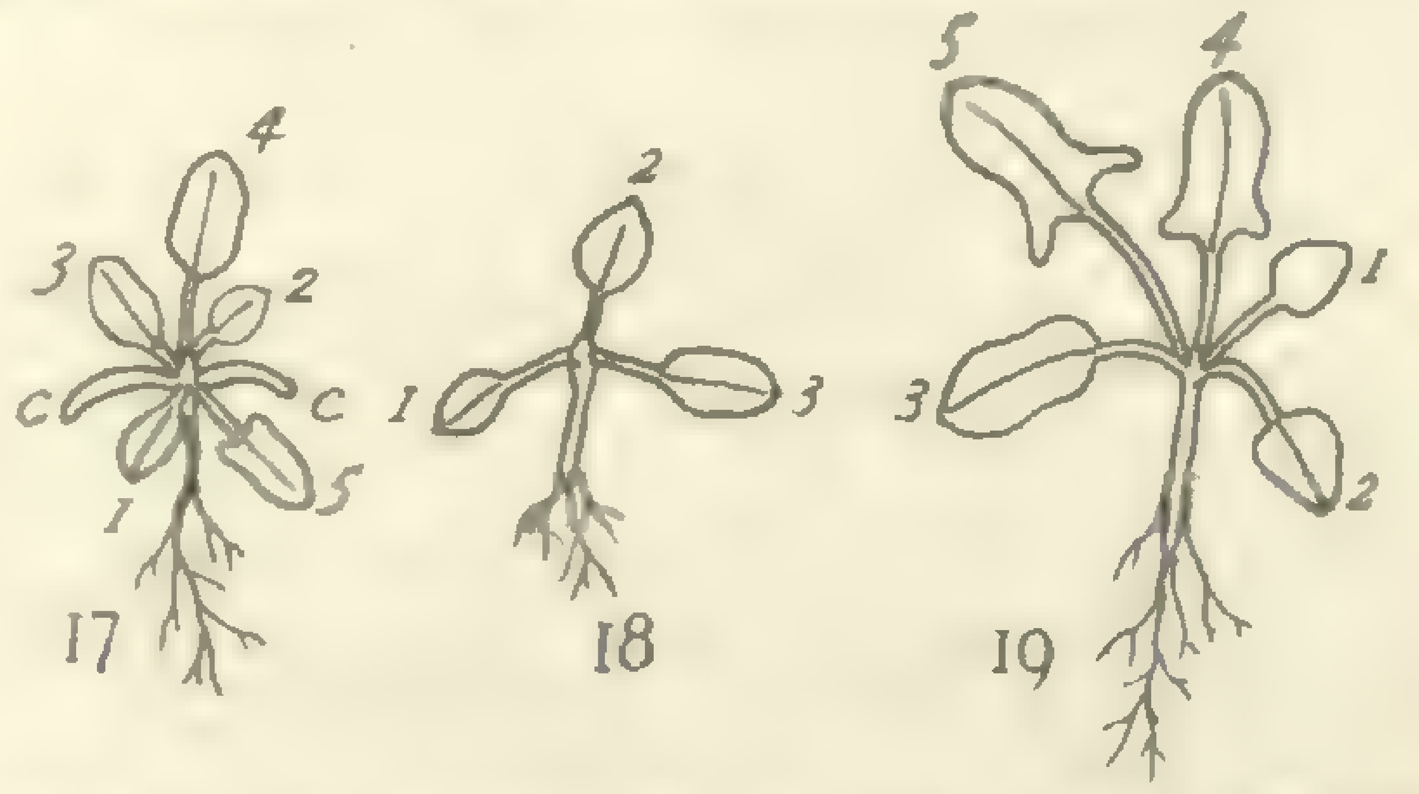
Rumex acetosella L. Figures 17–19.

(Sheep Sorrel.)

The peculiar auricled form of the leaves of this plant furnishes a means for study of stages, although the leaf is not compound as in the preceding cases. The seedling (Fig. 17) has the first and second nepionic leaves ovate, tapering somewhat at the base and with acute apices. In the third leaf the base is broader and the tip more blunt. The fourth leaf has a much broader base and more blunt apex so that it assumes a

roughly oblong shape. The fifth leaf has the auricled base characteristic of the species. Later leaves hold to this character. The early leaves of the seedling are red while later ones are green.

Turning to the early spring growth, very similar stages are noted (Fig. 18). In this weak plant the stages are exactly the same, leaf for leaf, as in the seedling after the cotyledons. In Figure 19, the early growth of a somewhat stronger plant, the first two leaves are similar to the first two of the seedling. The auricled form appears here in a vigorous plant in the fourth leaf, one stage earlier than in the seedling. The leaves in the early spring growth also resemble the seedling in their reddish color, but this is a superficial resemblance and not one of true repetition. It is dependent upon other causes.



FIGS. 17–19. — Seedling and early spring growths of *Rumex acetosella*. 17, seedling, showing cotyledons *c*, *c*, and first five nepionic leaves: 18–19, early spring growths showing stages by which the auricled form of base is reached.

On the flowering stalk there is a reduction of the base in the same manner, but in the reverse order, until below the flower there are linear leaves with narrow apices and bases. Thus the first leaves of the direct development in the seedling, the first leaves in the localized development in early spring growth and the last leaves in the reversionary localized senescence below the flower are without the auricled bases. In all other parts of the plant the leaves have the auricled base typical of the species.

Potentilla canadensis L. Figures 20–23.

(Common Cinquefoil.)

In this plant the seedling usually has the first nepionic leaf simple, the second ternate (Fig. 20). Succeeding leaves are ternate but apparently five palmate, due to the splitting of the lateral leaflets into two parts as shown in leaf 4 of Figure 21, a spring growth.

The early growth of this plant from adult roots is usually strong, but some plants have simpler leaves than characterize the adult. Over a hundred young plants were examined, all in an early condition of spring growth. Of these, the great majority had already the dissected ternate leaf, typical of the plant. Between fifteen and twenty of the smaller plants had the early leaves ternate, without dissection of the lateral leaflets (Fig. 22, leaf 2). In this specimen the first two of the early leaves had this character. In only one case in the hundred or more examined was a simple leaf found as the first of the early spring growth. In this specimen (Fig. 21) the first leaf was simple, the second ternate, and the succeeding ones of the typical dissected ternate form. This shows the rarity of this stage both in seedlings and spring growth, it being usually skipped by acceleration.

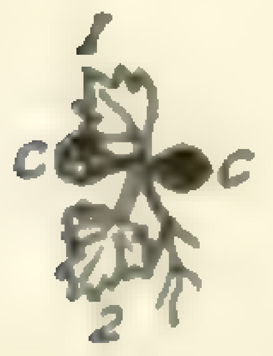


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FIG. 20.—Seedling of *Potentilla canadensis*, showing cotyledons, *c*, *c*, and first and second nepionic leaves, the first simple, the second trifoliolate.

In the flowering there is usually little reduction, for the flower is comparatively very small and not confined to the end of the shoot. The leaf from the axil of which the flower comes, may be reduced to simple ternate one, but in the specimens examined no further reduction was found. In the late season's growth, however, very definite senescence is seen (Fig. 23). Plants were obtained in late November, when the leaves were nearly or quite dead, where the last leaves were reduced very frequently, to a simple ternate form, as shown in leaf 5, Figure 23. In one case out of those of this late growth which were examined, there was a simple leaf as the last leaf of the season's growth (No. 6, Fig. 23). This leaf, the last of the senescent ones of the season's growth, is comparable to the simple leaf seen in the first stage in the direct development of the seedling, and also to the first leaf of the

21 22

FIGS. 21–22.—Early spring growths of *Potentilla canadensis*. 21, showing exceptional case where first leaf is simple.

23

FIG. 23.—Final season's growth of *Potentilla canadensis*. A rare case in which the last leaf, no. 6, is simple, due to lack of growth force at the end of the growing season.

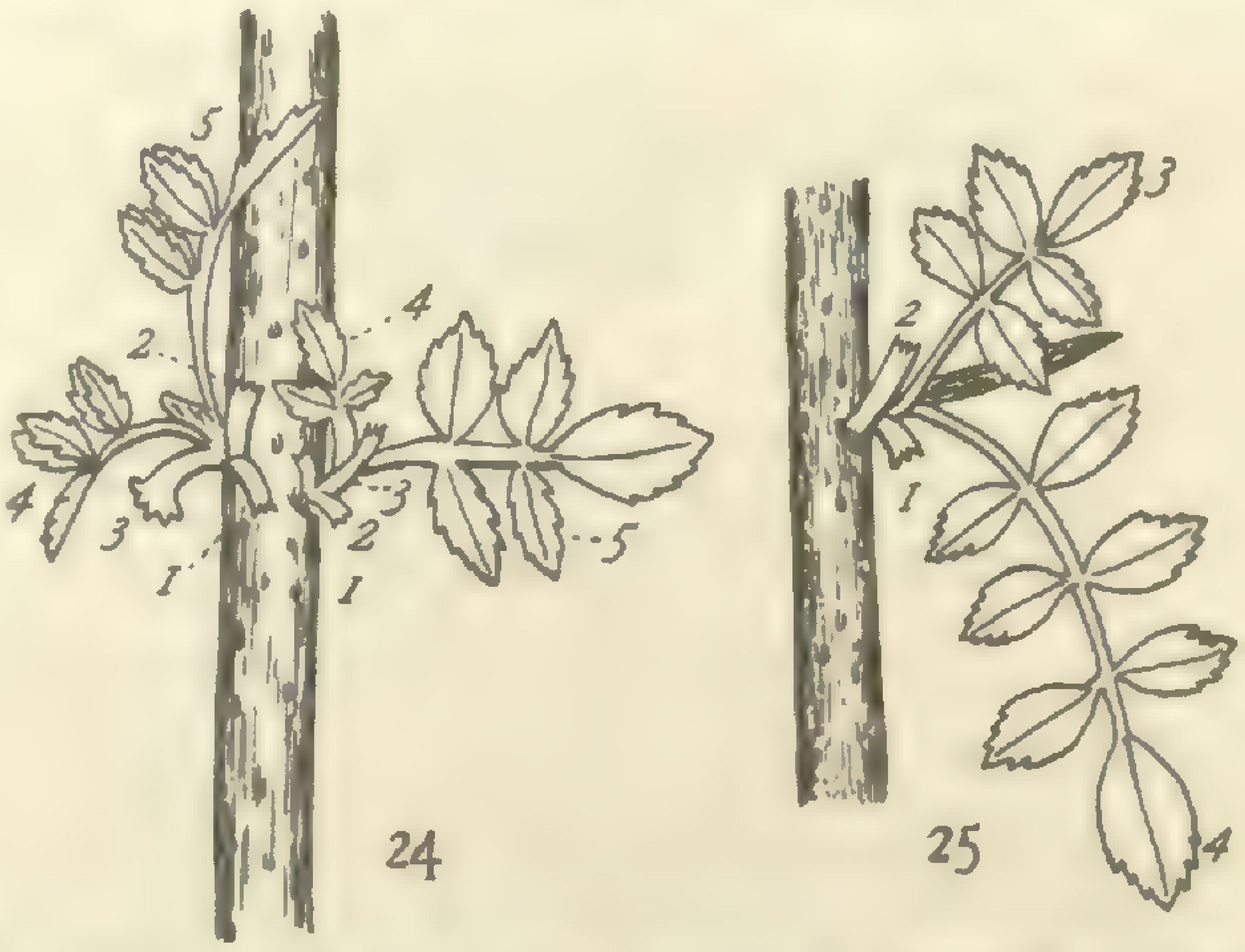
localized development, seen in the early spring growth. This is due to the lack of strength in the latest part of the season's growth and a consequent reduction follows. In this senescence then, the same stages are found, but they are developed in the reverse order.

Sambucus canadensis L. Figures 24–25.

(Common Elder.)

This seedling of this plant was not obtained, but one of another species, *S. nigra*, is figured by Lubbock (*Seedlings*, vol. II, p. 51, Fig. 420). In this species the leaves are in pairs. The two first pairs of nepionic leaves are simple, toothed, and the third pair is trifoliolate.

In the early spring growth of our species there are first, leaf-like bracts shown in Figures 24 and 25. These are notched or toothed at the distal end. In most cases there are three of these teeth or in some cases five. These teeth seem to represent the reduced leaflets of a compound leaf — in the commonest case a trifoliolate one. In such a case the first true leaf is trifoliolate or it may have five leaflets.



FIGS. 24–25. — Early spring growths of *Sambucus canadensis*. 24, showing the five toothed bract followed by a leaf with five leaflets.

In some cases, after the three-toothed bract there is a five-toothed one, usually more expanded and leaflike. Such a form is not followed by a trifoliolate leaf, but, in all the cases noted, by a leaf with five leaflets. These teeth then appear to represent the reduced leaflets, for if they did not there would be no reason against producing a trifoliolate leaf directly after the five-toothed bract. These bracts might be thought of as the stage representing a simple toothed leaf, but this definite succession of a leaf with five leaflets after a bract with five teeth seems to indicate them as reduced leaflets and not true teeth.

Beneath the flower there may be a very slight reduction in the number of leaflets, but as a rule it is not carried to any noticeable extent.

Chenopodium album L. Figures 26–36.

(Lamb's-Quarters. Pigweed.)

This very common weed shows excellent localized stages. It is an annual and therefore shows it simply in the localized senescence below the flower. The seedling (Fig. 26), shows the direct development. The first two nepionic leaves are narrowly oval, tapering at the base and apex, with the basal portion not broader than the similar apical portion. The third leaf has a broader base and in the fourth it has become decidedly angled. In succeeding leaves the base becomes angulate-toothed (leaf 9). This leads quickly to the adult character (Fig. 27), and is continued until flowering. Then comes the reduction shown in the series (Figs. 27–36). This series represents leaves in the axils of which branches or flowers are produced. The

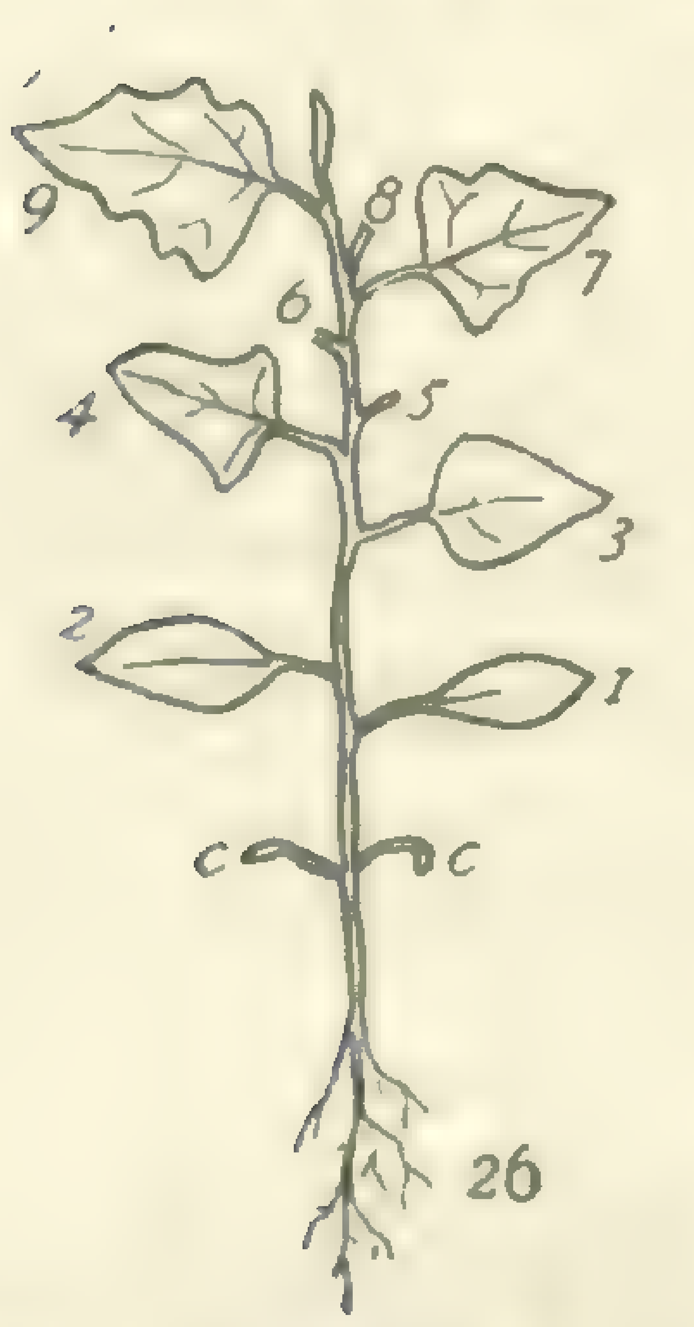
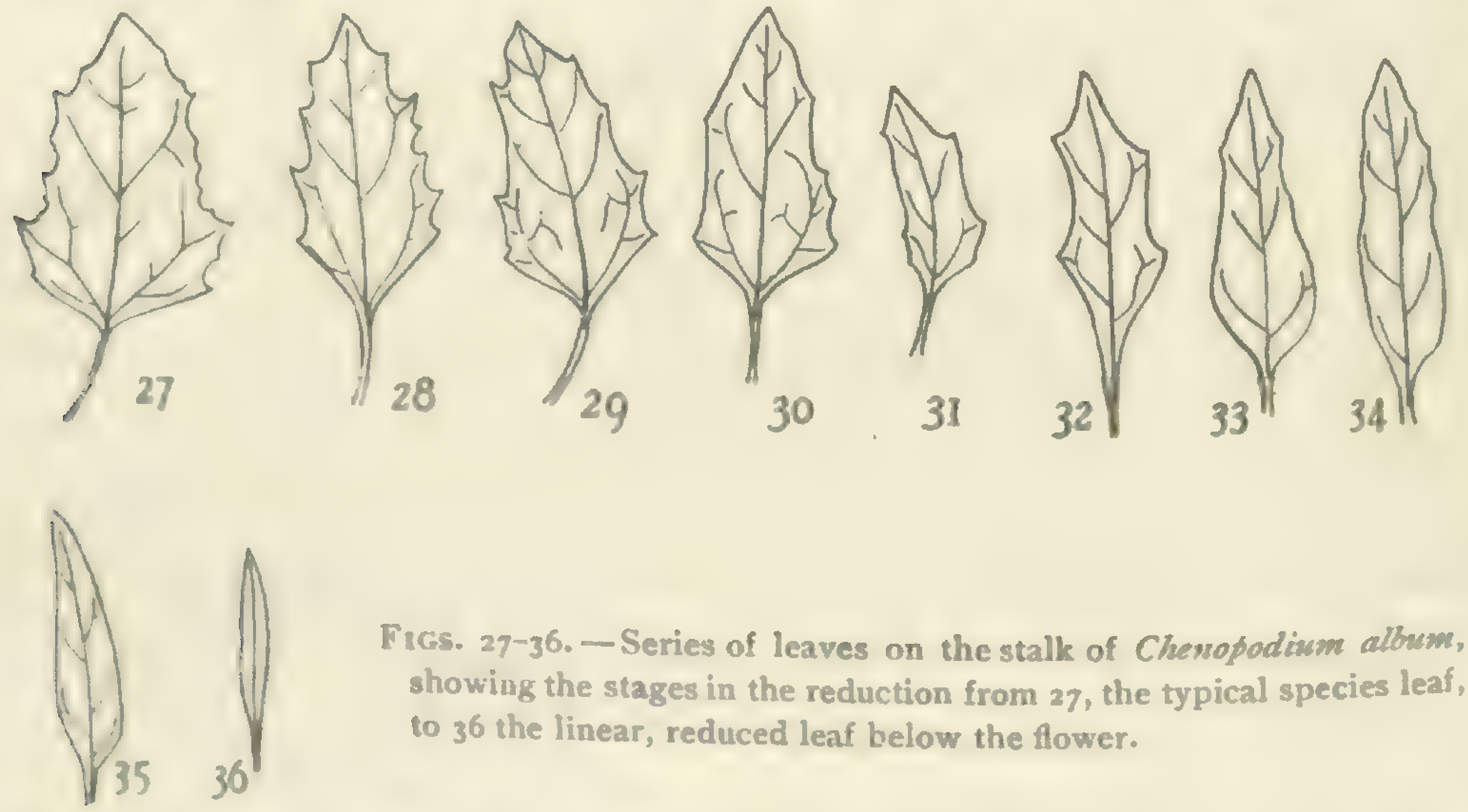


FIG. 26. — Seedling of *Chenopodium album*, showing cotyledons, *c*, *c*, and several of the nepionic leaves.



FIGS. 27–36. — Series of leaves on the stalk of *Chenopodium album*, showing the stages in the reduction from 27, the typical species leaf, to 36 the linear, reduced leaf below the flower.

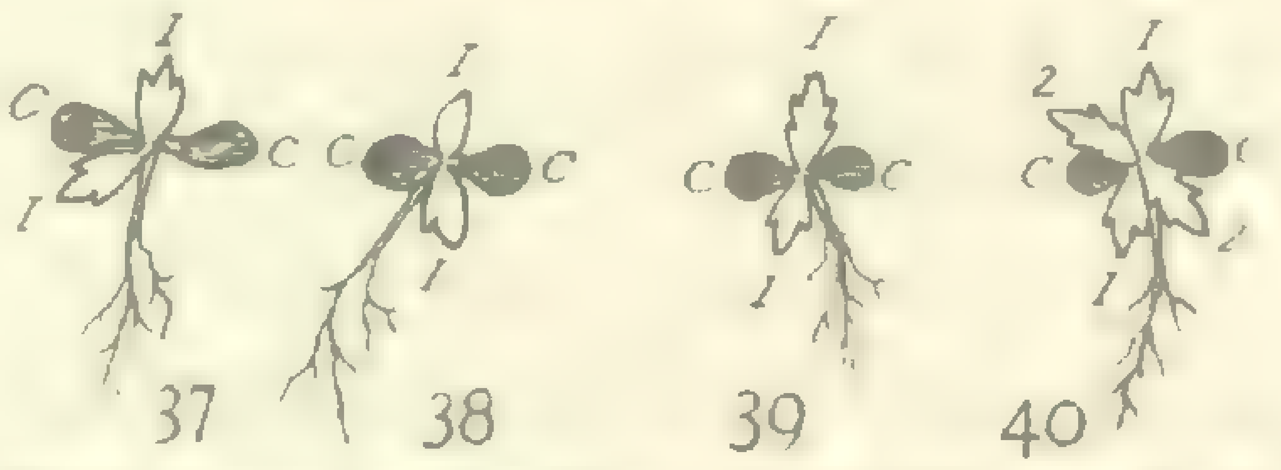
typical many toothed condition shown in Figure 27, is, in succeeding leaves, reduced until finally the simple leaves shown in Figures 35 and 36 are produced below the flower. The

stages passed through are very similar to those in the direct development of the seedling, but are in the reversed order of sequence.

Achillea millefolium L. Figures 37–42.

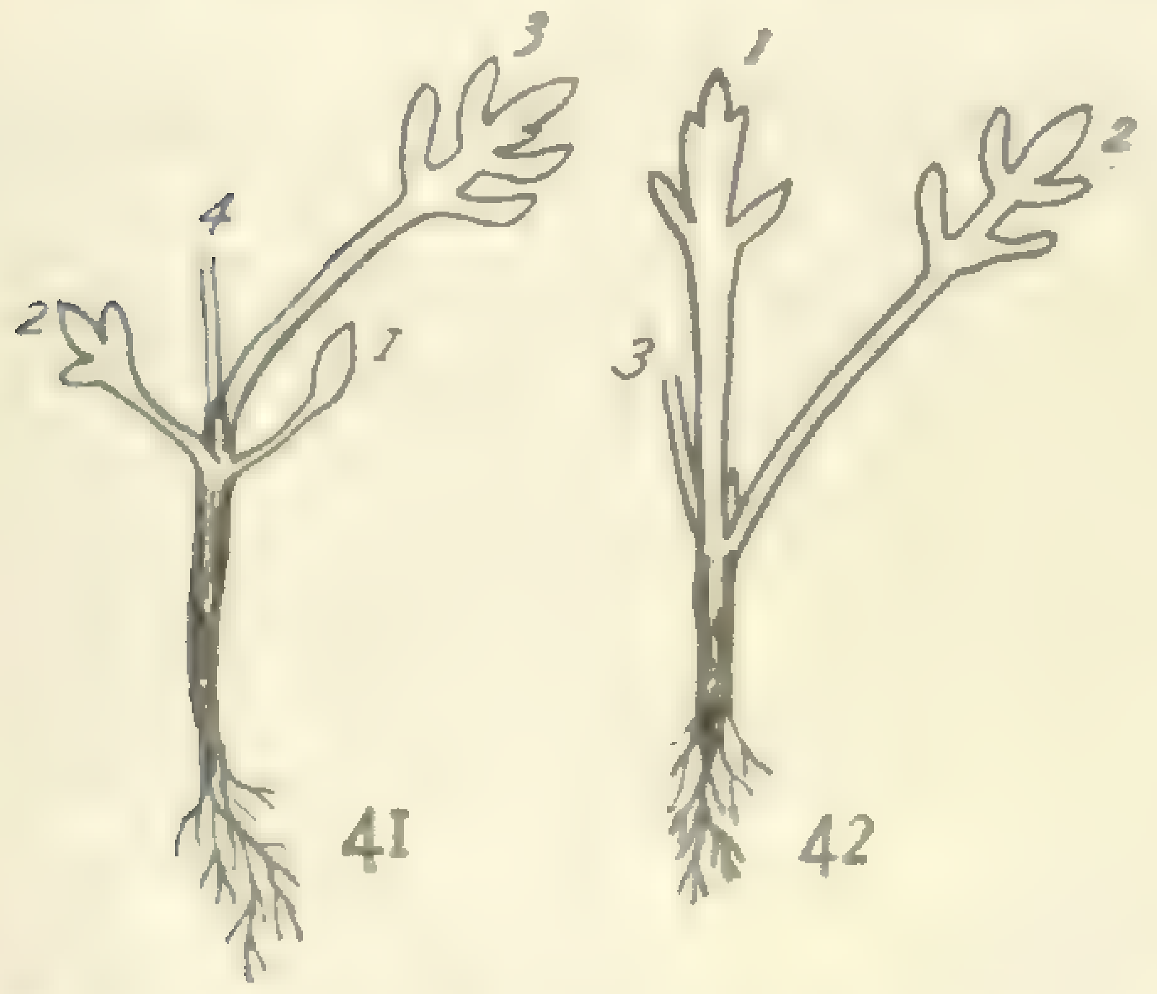
(Common Yarrow.)

The seedlings of this plant are very similar to those of *Tanacetum vulgare* L., as may be seen by a comparison of the figures of the seedlings of that plant (*Amer. Nat.*, vol. XXXVI, p. 881, Nov. 1902) with those of Achillea given here (Figs. 37–40). Both plants belong to the same tribe of the Compositæ.



Figs. 37–40. — Seedlings of *Achillea millefolium*, showing differential acceleration in different individuals. 37 and 40 showing normal individuals, 38 a retarded, 39 one that is especially progressive.

There is much variation in the seedlings as was also noted in Tanacetum (*loc. cit.* p. 871). The first pair of nepionic leaves are usually three toothed; the second pair five toothed (Fig. 40). As shown by the figures this may be decidedly varied. Figure 37 shows the typical first pair of leaves; Figure 40 in addition the typical second pair. Figure 38 shows a retarded individual where the character of a three-toothed leaf, usually taken on in the first pair of nepionic leaves has not appeared, except as indicated by a single tooth of one leaf. Figure 39 shows an accelerated individual where the character of a five-toothed leaf, characteristic of the second pair of leaves, is shoved back and appears in one leaf of the first pair.



Figs. 41–42. — Early spring growths of *Achillea millefolium*, showing differential acceleration in the localized development of two individuals, though both are more retarded than those usually found.

In the early spring growth better results were obtained than in the case of Tanacetum. Specimens of Achillea were found growing in the sandy railroad embankment which has been previously referred to. As in Tanacetum, the simplest leaves as a rule seem to be five toothed as in Figure

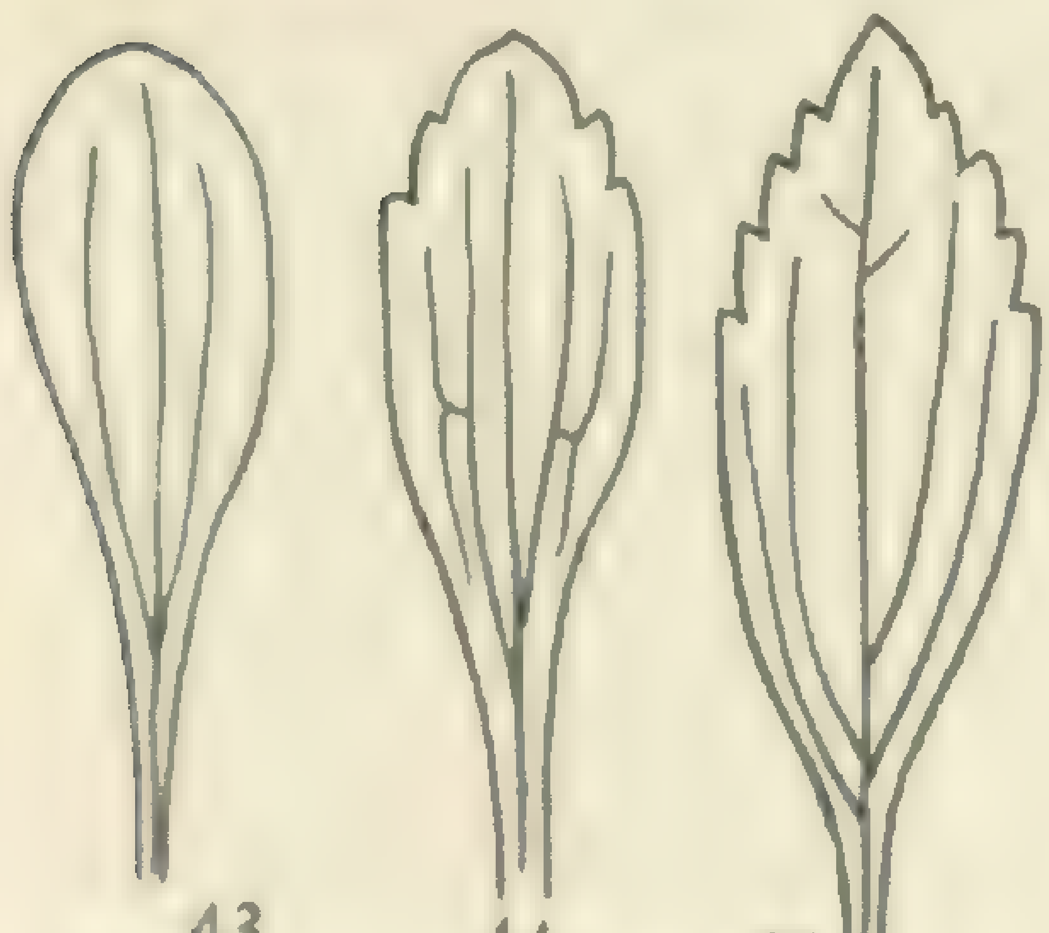
42. In rare cases, however, plants were found which had the first leaf with three teeth. In the specimen (Fig. 41), the first leaf was simple like one of the first nepionic leaves shown in Figure 38; the second was three toothed like the first nepionic leaves of the typical seedling (Figs. 37 and 40), and the third leaf has five teeth as was so commonly found as the first stage from rootstocks in the early spring growth. This then is a very retarded individual and repeats in its localized development, all the main stages seen in the whole series of seedlings representing the direct development.

Beneath the flower reduced leaves are also found. At the junctions of the stems of the compound corymb, leaves are found which are like those of the early spring growth and seedling in that they are simple and but few toothed. At the upper portion near the ultimate branchings are found leaves with five and three teeth and in some cases, simple entire leaves. These leaves are seen to repeat the same stages as in the localized development shown in spring growth and in the direct development of the seedling but in the reverse order. It is still another case of the localized reversionary senescence already referred to.

Aster acuminatus Michx. Figures 43–48.

(White Wood-aster.)

The seedling of this species was not obtained but a comparison of the early spring growth of an adult plant with the portion below the flower heads shows striking similarities. The stages are very simple, varying mainly in the number of the lateral teeth.



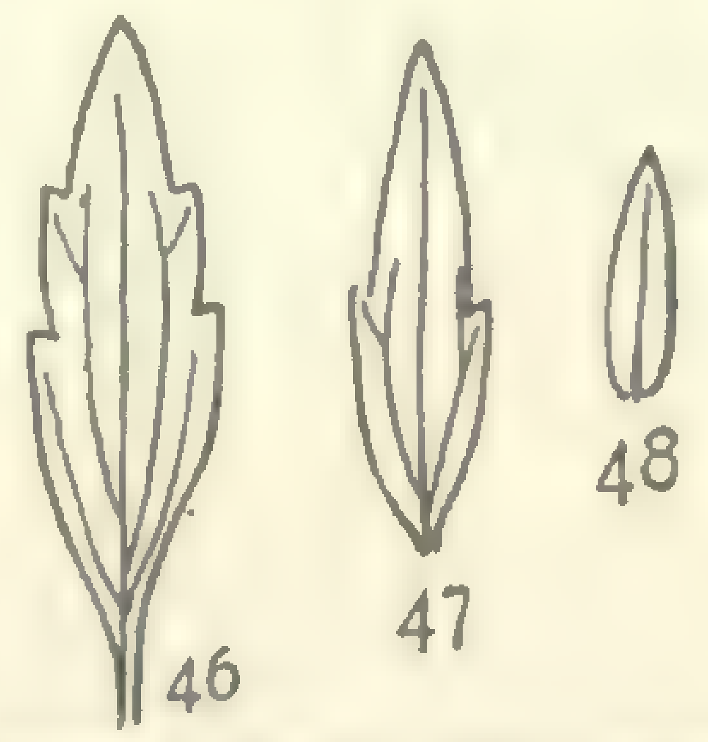
43 44 45

FIGS. 43–45 — Leaves of *Aster acuminatus*, showing three of the stages from the entire radical leaf 43, to the typical species leaf, 45.

In the early spring growth of a plant a year or more old, the radical leaves are at first entire and somewhat spathulate (Fig. 43). The next leaves have two lateral teeth and succeeding leaves have two lateral pairs (Fig. 44). In further development three lateral pairs are

produced and in the mature condition the leaves have four pairs, as in Fig. 45, which represents the typical leaf of the species.

Leaves like that shown in Fig. 45 are produced until the time of flowering. Then a reduction in the number of teeth takes place. Leaves with four, then three, pairs of lateral teeth are produced and nearer the flower heads, leaves with two pairs are shown in Fig. 46, later with the single pair (Fig. 47), and finally below the flower, the simple leaf shown in Figure 48. The reduction here is carried on in a definite manner and retraces exactly, in reversed order, the same stages that are passed through in the early spring growth, so that, using numbers for the lateral teeth, we may represent the stages graphically, calling the entire leaf number 1, as follows:



FIGS. 46–48. — The three final stages in the localized senescence below the flower of *Aster acuminatus*, 48 showing the last stage in the reduction.

Early spring growth	to	Flowering
1, 3, 5, 7, 9 .	. . . .	. 9, 7, 5, 3, 1.

Eupatorium perfoliatum L.

(Thoroughwort. Boneset.)

This well known plant shows in its leaf characters certain things which may be noted here as in the same line with the preceding cases. The main leaf character of this plant is the connate-perfoliate form of the leaf. This, however, by an examination of a flowering specimen, will be seen to occur on only a part of the stem. In the early spring growth of the plant, the bases of the opposite leaves are free and narrow. Later the coalescent form is taken on and kept until well toward the flowering. Then the early form is again taken on, the base of the leaves being narrowed and failing to meet.

A variety of this species, var. *cuneatum* Engel., is apparently a more primitive form. It keeps the early character throughout its life history, the leaves failing to coalesce at their bases. This variety also has fewer flowered heads than the typical form of the species.

The commonest plants illustrate well the principle of localized stages in development seen in the direct progressive development of the seedling, in localized stages of spring growth and in the localized senescence at flowering. It may be shown in a variety of ways, as noted in the present paper. In Thalictrum, Baptisia, etc., it was shown especially by change in the number of leaflets; in Rumex, by the changes in the auricled base; in Daucus, etc., by the change in the number of the teeth, and finally in Eupatorium, by the presence or absence of the connate form of the leaf.

Different individuals show variations due to differences in acceleration of development. There is a differential acceleration in individual seedlings, shown where the first nepionic leaf in various individuals is more progressive or more retarded than in the typical cases. In spring growth it is also shown in much the same way, and with a still wider range of variation. These differences in acceleration may be caused by poor conditions, such as poor soil, lack of sufficient moisture, cold, etc., and by internal causes not accounted for in the above.

Regressive development, seen in the localized senescence below the flower, is shown in many cases to be more reversionary than stages in the usual seedling. When a large number of seedlings are examined, however, such extreme cases of variation may be seen which would otherwise be overlooked.

Boston Society of Natural History,
May, 1904.

AN ARRANGEMENT OF THE FAMILIES AND THE HIGHER GROUPS OF BIRDS.

R. W. SHUFELDT.

Birds constitute a class of the phylum Vertebrata, and belong to the branch Craniata. Above the latter subphylum they are associated with the Reptilia in the tribe Sauropsida, which last in time has divided into two now distinct classes, namely, Reptilia and Aves (see *A Classification of Birds, postea*). Of all the existing vertebrate groups, birds are, morphologically speaking, the most homogeneous; probably none of the phyla recognized by zoölogists are more so. There is a very considerable gap between a thrush and an ostrich, but it in no way compares, in the matter of profundity, with the gap that stands between man and the duckbill, or between an elephant tortoise and a garter snake. This morphological homogeneity in birds by no means renders their taxonomy any the less difficult for us; indeed, for very obvious reasons it greatly tends to enhance the intricacies of the problem. This fact is now so generally appreciated by avian classifiers that it is quite needless to discuss it in the present connection.

To classify birds correctly and to point out the natural relationships and interrelationships of all the species and subspecies now in existence we resort to various lines of research and employ data of widely different nature. In the field of palæontology we meet with a mass of material, the comparative study of which has led to the conviction that Aves and Reptilia have arisen from a common stock. The indications of this have by no means died out in certain existing representatives of these two classes of the Sauropsida. For example, it is quite apparent when we come to trace the ancestry of the existing ostrich and its surviving allies in various quarters of the globe. The trend backward in time is distinctly reptile-wards and eventually brings one to the consideration of a long-extinct assemblage of

forms from which not only have the ostriches arisen, but both modern birds and reptiles have been derived.

In the classification of existing birds, again, we have recourse to their anatomical structure or morphology, and incidentally their physiology to assist us, the first of these being a very powerful aid. By morphology is meant the science of the outer form and internal structure, and to be of practical value in taxonomy it must be made thoroughly comparative. As far as possible we also study the morphogenesis of birds or the genesis of form in their case through evolution. Of great assistance is the knowledge we derive from our researches into the comparative ptilosis and pterylography of the group and all that pertains to these related sciences. In our efforts, too, to seek out the true relationships of birds in order to arrive at a natural classification we must take into consideration, in the broadest possible sense, their embryology; their oölogy and nidiology; their habits and comparative longevity, and even their various notes and songs must be given due weight. Their geographical distribution, a very important factor to be studied in their taxonomy, is to be considered not only from the viewpoint of the present distribution of the species of the class over the earth's surface, but likewise a comprehension, as far as possible, of the question as to how that distribution came about. The data for the latter, in the case of birds, are extremely meagre, as it takes into consideration the migration and original habitats of various forms of the class during geologic times, and as but very few fossil remains of birds have been discovered in any part of the world, there has been in consequence but very little light thrown upon this latter side of the question. So far as it goes, however, it has its value, as has also, to some extent, a consideration of the migrations, *per se*, of existing species and subspecies.

In some of these sciences, as in the case of ptilosis and pterylography for example, not only must both sexes be studied and compared, but the young at all stages of their existence. Both ptilosis and pterylography furnish very useful data to assist us in the classification of Aves, and as exponents of a bird's topographical anatomy, for this purpose they are quite co-equal in the matter of importance with the osteological system of the internal

structure; indeed, ptilosis, pterylography, and osteology stand among the most important factors at our command, in the

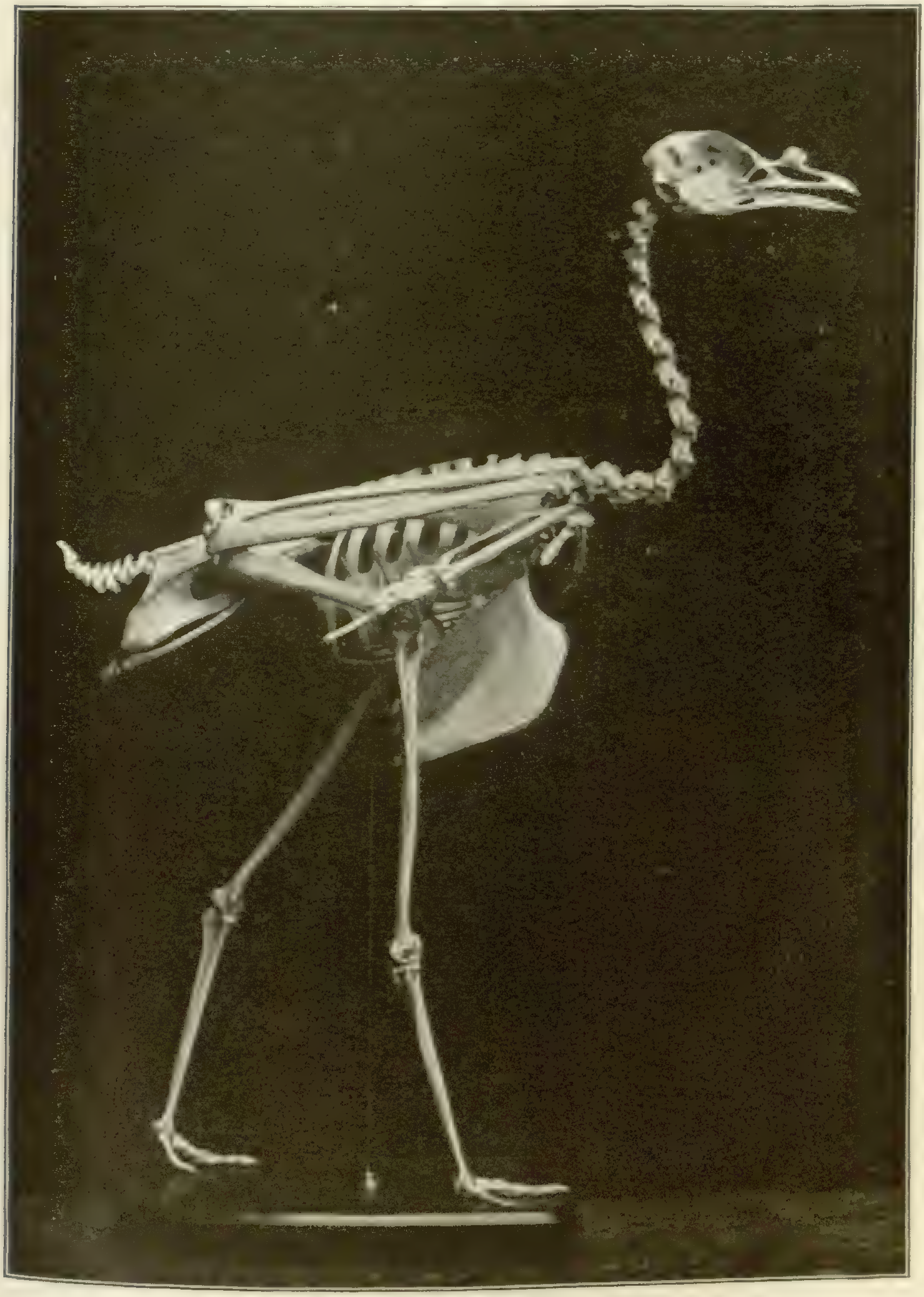


Fig. 1.—Skeleton of the Great Bustard. *Otis tarda* Linn. The enlargement on the upper mandible is abnormal. Coll. Natl. Mus. No. 12,315.

economy of this group of vertebrates, that become available in their classification. Right here it will be as well to state, how-

ever, that we will never arrive at the true and natural classification of birds, through the employment for that purpose of any *single set* of morphological characters.

A study of the skeleton in birds, for example, carries us a long way toward an understanding of their various alliances and relationships; this is particularly the case on account of what is to be derived from avian palæontology, — the bones being, with few exceptions, the parts preserved. It is extremely unsafe and dangerous to the science of this subject, however, to thus employ the osseous system alone. The taxonomical scheme based upon such knowledge should be modified and corrected by the employment of every other fact, every particle of information that has been made known in the matter. To this end various characters that have been found to exist in the muscular, the arterial, the digestive, the nervous and other systems have proved to be of considerable use.

A comparative study of the beaks and feet; the various characters presented on the part of the plumage, especially as to color, structure, and style, often constitute admirable checks on a classificatory scheme of the class based on osteological data. Food and other habits when properly studied, and the results applied, are also efficient aids to establishing many of the primary divisions in our scheme; and a consideration of such data without reference to facts of any other kind, is sufficient to enable us to refer a duck, a hawk, or a thrush to their proper places in a taxonomical arrangement. In other particulars nidiological and oölogical studies are of value taken in connection with the anatomical and other ones enumerated. Some birds build no nest at all, others construct them of all manner of shapes and sizes and out of all manner of materials. Some birds lay but a single egg, while others may lay a dozen or more; some eggs are plain white and unspotted, others are of other colors and unspotted, still others are variously marked or possess other peculiar characters, — all such facts, however, when properly comprehended and assorted, may be employed in classification with distinct advantage. For example, certain birds possessing an association of osteological characters in their skeletons lay but two white eggs in an elaborately constructed arboreal nest.

while no other existing birds of the class Aves have a similar association of characters and habits. Here then nidiological and oölogical facts support and emphasize osteological ones in establishing affinities. Again, were we told that we had before us the

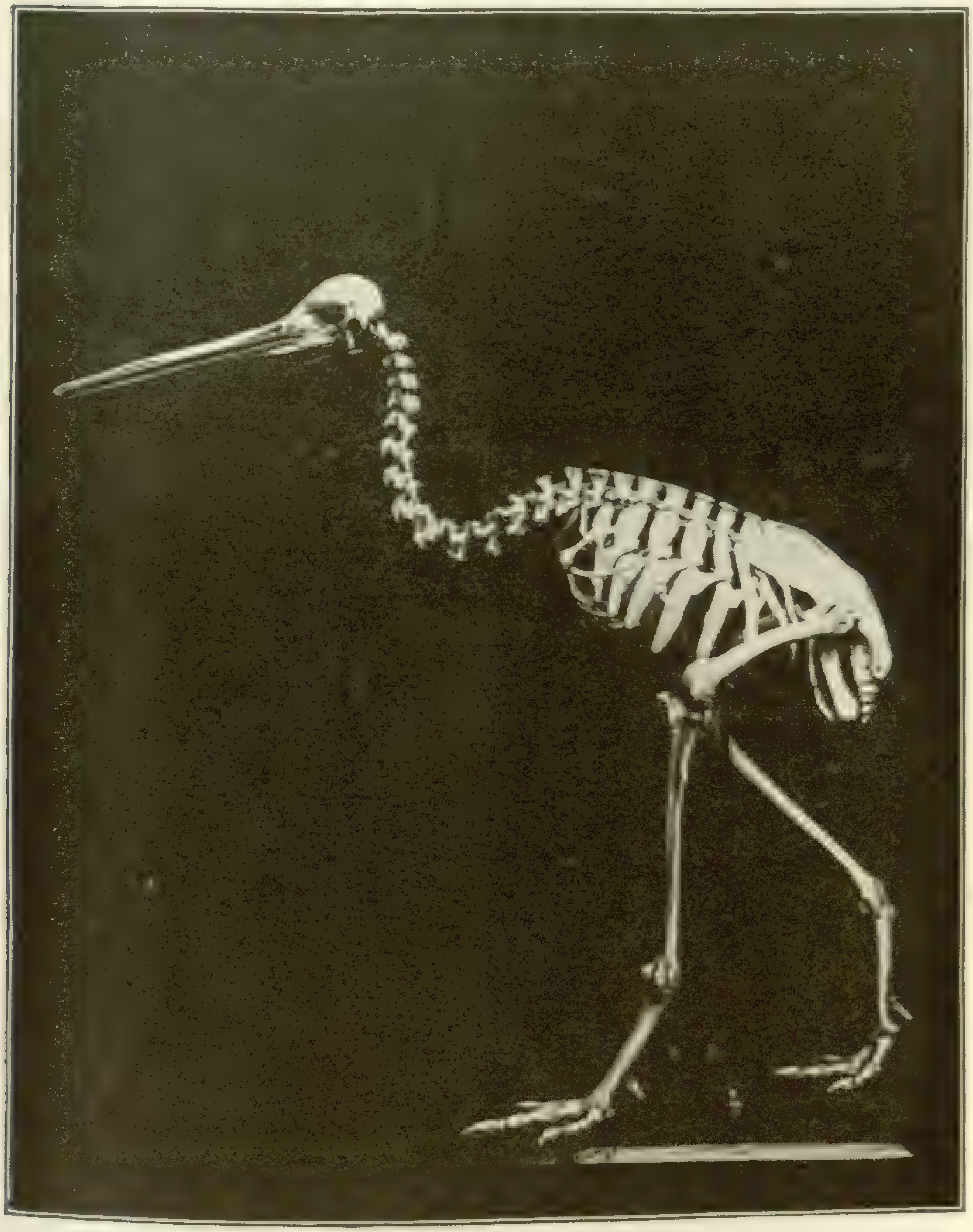


Fig. 2. — Skeleton of the Kiwi, *Apteryx australis* Shaw. Coll. Natl. Mus. No. 11,416.

skeletons of two *small* birds *in each* of which the osseous mandibles were slender and short; the nasals holorhinal; the basipterygoid processes absent; while in the sternum the keel was

well developed, and the posterior margin of the body of the bone presented *no notches whatever*, we would be quite at a loss to say what the two species were, but the moment that we added to these osteological characters the fact that it was also known that in the case of one bird it laid its *single* white egg in a burrow in the ground, while the other laid *several* white eggs in a little basket-like nest built by itself and found within the cavity of some great hollow tree, we would not hesitate to say but what the skeleton of the first belonged to some one of the smaller petrels, and that of the second to a swift, and very possibly a Chætura. Your opinion is considerably strengthened when you are told that the bird laying the single white egg had webbed feet, and was strictly a marine species, while the other possessed no such character of the feet, and was a typically insectivorus aërial land bird. When still other characters from other anatomical systems and parts are added, the true relations of the two species can be fixed with absolute certainty. In the present instance they chance to be very remote, although this by no means seemed to be the case when only the few osteological characters were mentioned. Such researches place forms in their proper groups, but to decide upon, or to discover the true relationships of, the families and main groups to each other is an entirely different matter and infinitely more difficult.

It is very important indeed that we should thoroughly comprehend the origin and evolution of such an assemblage of vertebrate forms as birds, and it is highly important, too, that we classify existing birds in such a manner that our classification conveys to the mind not only an orderly arrangement of our knowledge upon this subject, but a scheme representing as near as possible the actual and natural relationship of the major and minor groups of birds as they now exist. To convey such a scheme to the mind various plans and methods have been proposed and adopted by a number of ornithological taxonomers at different periods of the history of the science. It is not necessary that all of these be described here,— a few of the more prominent examples will answer our purpose. In his memoir "On the Osteology of Gallinaceous Birds and Tinamous," read before the Zoölogical Society of London on the 25th of

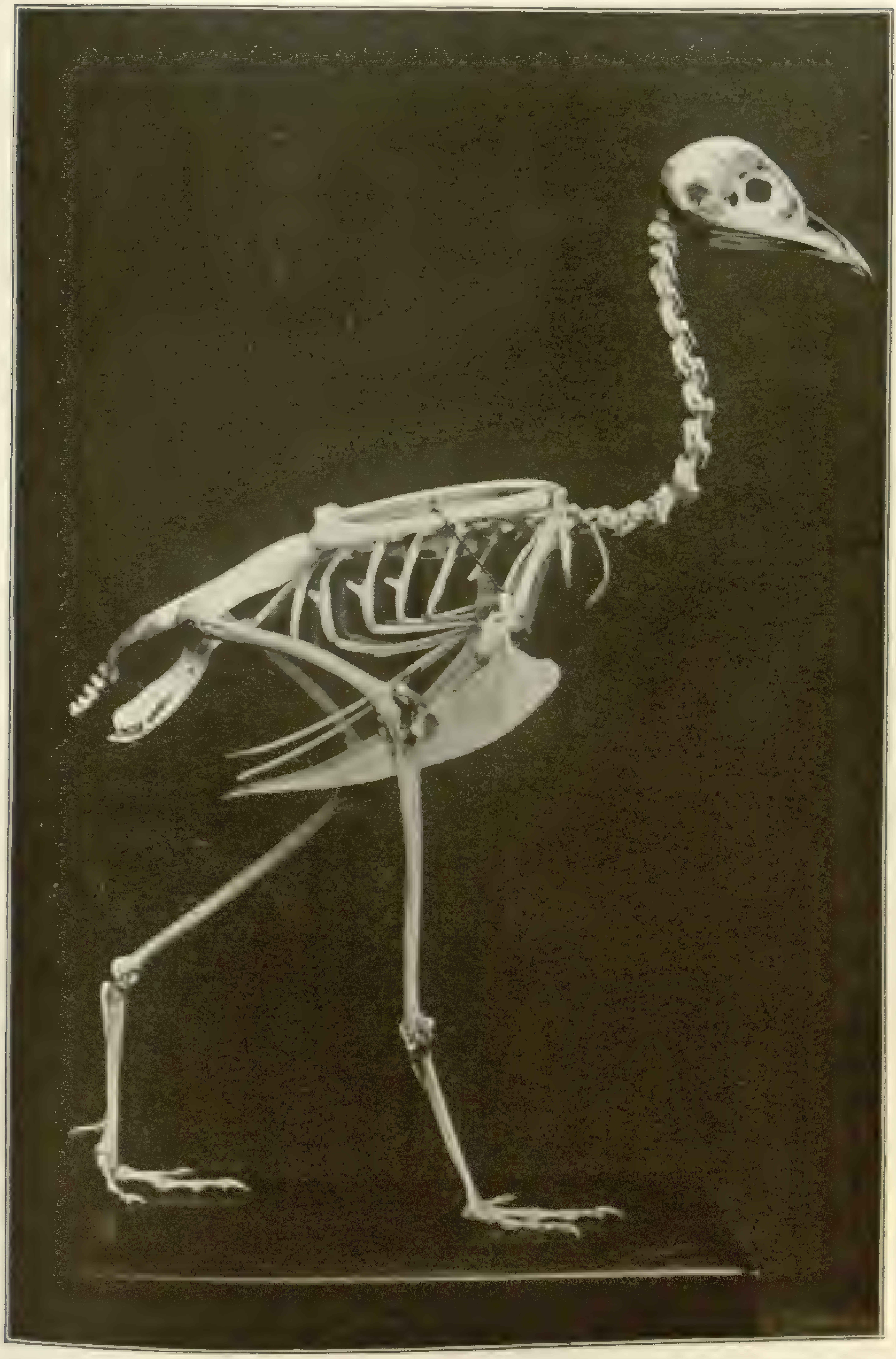


Fig. 3.—Skeleton of the spotted Tinamou, *Nothura maculosa* Temn. Coll. Natl. Mus. No. 17,949.

November, 1862, Professor Wm. Kitchen Parker gives us one of the earliest methods of setting forth in print the relationships of a number of birds treated of in the work named. These had to do with genera and not with families, and he conveyed his ideas on their relationships in two ways. One of these consisted in a method of what might be termed grouping, and the other the columnar method, or as it is sometimes called, the "linear," for the fact that the genera, or families, or the higher groups are printed in a linear sequence following in an order determined by what is supposed to be their relationships. Thus Parker said in the above quoted memoir on page 235, "I will first show, in two parallel columns, how both the Fowls and the Rails run insensibly through certain leading genera into the lowest (reptilian) types of diving-birds."

Notornis	Gallus
Brachypteryx	Crax
Ocydromus	Talegalla
Tribonyx	Palemedea
Crex	Anseranas
Rallus	Plectropterus
Gallinula	Anser
Porphyris	Anas
Fulica	Fuligula
Podilymbus	Harelda
Podiceps	Biziura
Podica	Merganser
Aptenodytes Phalacrocorax	Colymbus Alca

This method has its advantages, also its many disadvantages, and Parker felt the weight of some of these when he placed at the foot of the first column Aptenodytes aside from but near to Phalacrocorax, and in the second column Colymbus aside from Alca. So on the very next page or two (236, 237) he resorts to the grouping method and uses it in the case of Pluvialis, Talegalla, Hemipodius, Syrrhaptes, and Tinamus. This plan is well shown in the case of the last named genus,— thus :

FIG. 4. — Skeleton of the Hoatzin, *Opisthocomus cristatus* Gmel. Coll. Natl. Mus. No. 18,518.

	Gallus	
Charadrius	Dendrortyx	Ocydromus
Syrrhaptes		Hemipodius
	TINAMUS	
Apteryx		Rhea
	Casuarius	
MAMMALIA		REPTILIA

It is very evident that such a method of grouping could never be adopted, for to treat in general *all* the genera in any such a manner would certainly fill the subject with confusion, and the same would apply to the families being dealt with and printed according to any such an arrangement. It answers fairly well in the case of exhibiting the relationships of a single genus or other group, and for this purpose it has been adopted by some. A modification of this scheme consists in joining the names by *straight lines* in order to render the kinships more evident. This doubtless led to the use of the phylogenetic tree, a plan which will be more fully described farther on. In the matter of the linear method, with various modifications it has been employed by not a few avian taxonomers. Sharpe arranged Huxley's (1867) classification of Birds in this way in his now famous paper entitled, "A Review of Recent Attempts to Classify Birds" (1891, p. 4); Garrod resorted to it, and so did Sclater. Alfred Newton did to a limited extent, while Reichenow, Stejneger, and Fürbringer have presented complete schemes of avian classification in this manner,— Reichenow and Fürbringer employing the phylogenetic tree in connection with it. To some extent Seebohm also used the linear method, and Sharpe illustrating the latter employed a "diagrammatic map" giving the Seebohmian "Orders" in small circles, these circles bearing certain relations to each other, which relations were supposed to represent in a way, and convey to the mind, the relations the groups of birds themselves bore to each other. Finally these orders were surrounded by broken lines in such a manner as to show the kinships and connections of the subclasses found in Seebohm's scheme (*loc. cit.*, pp. 44–48). Sharpe also in his "Review" gives us an admirable example of the linear scheme

FIG. 5.—Skeleton of the Rhinoceros Hornbill, *Buceros rhinoceroides* Temn. Coll. Natl. Mus. No. 18,755.

of classification, and this is rendered vastly more useful from the fact that many of the *characters* of the suborders are conveniently footnoted in the same arrangement. He also employed the 'circle system' in several plates in his memoir, as well as a modification of the 'radiating line system,' and both with more or less effect (Plates IX–XII). This plan of presenting group characters is excellent in many particulars, and in connection with a modified linear scheme it has been employed by Cope in his Classification of Aves (*Amer. Nat.*, Vol. XXIII, No. 274, Oct., 1889, p. 869), and also by Hans Gadow (*P. Z. S.*, 1889). Still earlier than these it was used by Garrod (*P. Z. S.*, 1874).

Turning to the plan of the 'Phylogenetic Tree,' it has, among other authors, notably been employed by Reichenow (*Vögel. der Zoologichen Gärten*, 1882) and Max Fürbringer ("Untersuchungen zur Morphologie und Systematik der Vögel": '*Bijdragen tot de Dierkunde*,' Amsterdam, 1888. Tafln XXVI, XXVII). Reichenow's "Tree" is a very crude representation, and needs no special description in this place. It has, however, an historical interest for us, and a good copy of it may be found in Dr. Sharpe's 'Review' on page 23. A far more elaborate and widely known representation is Fürbringer's 'Phylogenetic Tree of Birds.' This brings up the main stem from the reptilian root-stock, from which, as it ascends, are thrown off the now dead limbs of a number of more or less known or even hypothetical groups of avireptilian or reptilioavian forms. Farther up, more extensive branches carry out the evolution of the main ostrich types, and soon above these the generous and complete development of the tree,—its many more or less closely dividing and branching limbs, boughs and stems, showing all the main modern or existing groups as they are supposed to have been given off from each other, or else to have arisen from the main trunk. This tree is horizontally divided by imaginary planes at certain points, dividing it into upper, lower and middle sections or horizons. Viewing the projections of these vertically we have the circular sections of the various branchings of the tree before us, and these will again give the relations to each other of the various groups. Three such projections are

obtained, which Fürbringer has represented for us upon three plates. The horizontally divided stems produced by these cutting planes are also grouped by a system of three kinds of

Fig. 6 — Skeleton of the Red-billed Toucan, *Rhamphastus carinatus* Swainson. Coll. Natl. Mus. No. 17,315.

surrounding lines which associate, in the opinion of this eminent authority, the minor and major groups in such a manner as to

have them furnish the requisite data upon which the linear scheme of this classification has been based. Without any manner of doubt this is the most elaborate provisional scheme of the classification of Birds extant, and beyond all question, in most particulars, the relationships of the groups as therein represented are correct, and, as far as possible, convey to our minds what has taken place in their evolution.

In setting forth a scheme of classification, the principal objection to the linear method is that it does not properly represent the branching or the derivation of new groups in time as the taxonomer has them in his mind. It brings some groups too close together, throws others too far apart, and in some instances in the lineal descent interpolates groups among others in such a way as to either do violence or misrepresent the true affinities and relationships of the forms as they exist or have existed in nature. By the employment of the phylogenetic tree we obviate a great many of these objectionable features so dangerous to the credit of a natural classification. Still notwithstanding all this, the *linear* method has been adopted in the present memoir, and for the reason that it is believed that the time is not yet at hand again, when the making of another elaborate phylogenetic tree for birds would be considered justifiable as we are still in the provisional stage. Therefore it has been adopted here. Further, it has been thought better to weave into this scheme such fossils of extinct types and species of birds as have come to hand, and this has likewise been done. For the rest, I have been influenced in the classification here set forth by my having read the literature of ornithology since boyhood; by my having studied everything that pertains to birds for a period extending over thirty years. This study has been constant, and has been undertaken in the field, in the closet and in the dissecting room. It has been devoted to every department of ornithology and of ornithotomy and morphology.

These studies have been supplemented by similar studies in the structure and habits of many mammals, reptiles, batrachians, fishes and other groups. These latter researches have convinced me that to render the matter of classification more homogeneous with respect to the vertebrate in general, or in fact to express

the conditions as they really occur in nature, the Class Aves is susceptible of being divided into but *two* orders, — the first or Order I, including the SAURURÆ, and the second, or Order II, including all other bird-forms, whether extinct or existing, that do not belong to Order I. This Order II is known as the ORNITHURÆ. There can be no possible doubt but what in the early history of birds these two orders arose from the same general ancestral stock, but during the geologic ages that have followed since, myriads of species have become extinct and the remains of this vast host have never, save in a few isolated instances, ever been found or seen by us. Hence the profundity of the gap now existing between the Saururæ and the Ornithuræ. As wide as this gap is, however, the discovery of a very few of the extinct and intermediate types would tend to greatly lessen its width. Nevertheless, we must classify the forms as we have them, and as we find them, and to do this consistently we must recognize the two orders aforesaid.

Fürbringer in his classification considers the Saururæ and the Ornithuræ each to represent a subclass. In this I cannot agree with him. Birds offer no such division, and are, as a matter of fact, too homogeneous in their structure to admit of it.

The Saururæ, as is well known, are at present represented by that unique, if it be unique, form Archæopteryx of the family Archæopterygidæ. There is every reason to believe that there once existed higher divisional groups of this family, therefore the order Saururæ is here subdivided into the supersuborder Archornithiformes and the suborder Archornithes (see "A Classification of Birds," *postea*). As thus created this order is capable of admitting into it any other fossil genus or genera of birds allied to Archæopteryx, whether they come from the Jurassic age of the Mesozoic epoch of Bavaria or from any other geologic horizon in any other part of the world. So far as is at present known they represent the oldest avian types in the hands of science.

The classification of birds set forth in the present memoir carries the arrangement down to include the families only, while for the higher groups, intermediate between the order and the family, I employ the superfamily, the suborder and the super-

suborder. To my mind such divisions can be very profitably employed to express the normal relationships of birds as they exist, and the relative nearness to each other of the various groups as compared with other natural assemblages of the Vertebrata.

Passing now to the consideration of the second order of birds (Order II, Ornithuræ) we meet at first with the array of the so-called ostrich forms it contains, or supersuborder II. These represent some of the lowest types of existing bird forms, and a number of extinct species allied to them have been discovered. It will not be necessary to discuss the systematic position of the Dromæognathæ (supersuborder II) for the reason that I have already recently done so in a paper published in *The American Naturalist* (Vol. XXXVII, No. 433, January, 1903, pp. 33–64. 2 figures), and this likewise applies to the supersuborder III, the Odontoholcæ. The Odontoholcæ are placed next in order after the ostrich-forms not for the reason that they possessed anything in their osseous systems that in any way connected them with the Dromæognathæ, but because they represent the archaic ancestral stock from which has been derived the existing Supersuborder Colymbo-Podicipitiformes (IV) containing the loons, divers, and grebes, and these last in the matter of organization stand among the lowest of known types of modern birds.

This group has been thoroughly treated in my published papers. A few of the more important groups, however, are still in press, as for example the "Osteology of the Accipitres" (Carnegie Museum); "Osteology of the Anseres" (Carnegie Museum); and the "Osteology of the Lariformes" (complete in manuscript). I now offer my scheme for *A Classification of Birds*. This classification requires in some of the groups illustrations in the way of bird skeletons that I have heretofore been unable to publish, and which will throw additional light upon the subject. These have been kindly photographed for me at the U. S. National Museum at Washington, and reproductions of those photographs are herewith presented, with the necessary descriptions.

A Classification of Birds.

Phylum :—
Vertebrata.
Branch :—
Craniata.
Tribe :—
Sauropsida.
Classes :—
Reptilia.
Aves.

Class Aves.

Order I. Saururæ.

Supersuborder	I.	Archornithiformes.
Suborder	I.	Archornithes.
Family	I.	Archæopterygidæ.

Order II. Ornithuræ.

Supersuborder	II.	Dromæognathæ.
Suborder	II.	Struthionithes.
Family	I.	Struthionidæ.
Suborder	III.	Rheornithes.
Family	I.	Rheidæ.
Suborder	IV.	Casuariornithes.
Family	I.	Dromaiidæ.
	II.	Casuariidæ.
	III.	Dromornithidæ.
Suborder	V.	Dinornithes.
Family	I.	Dinornithidæ.
Suborder	VI.	Æpyornithes.
Family	I.	Æpyornithidæ.
Supersuborder	III.	Odontoholcæ.
Suborder	VII.	Pygopoformes.
Superfamily	I.	Hesperornithoidea.
Family	I.	Enaliornithidæ.
	II.	Hesperornithidæ.

Supersuborder	IV.	COLYMBO-PODICIPITIFORMES.
Suborder	VIII.	PYGOPODES.
Superfamily	I.	Podicipoidea.
Family	I.	Podicipidæ.
Superfamily	II.	Urinatoroidea.
Family	I.	Urinatoridæ.
Supersuborder	V.	APTENODYTIFORMES.
Suborder	IX.	IMPENNES.
Family	I.	Spheniseidæ.
	II.	Cladornithidæ.
Supersuborder	VI.	PROCELLARIIFORMES.
Suborder	X.	TUBINARES.
Family	I.	Procellariidæ.
	II.	Puffinidæ.
	III.	Pelecanoididæ.
	IV.	Diomedeidæ.
Supersuborder	VII.	PELECANIFORMES.
Suborder	XI.	STEGANOPODES.
Superfamily	I.	Pelecanoidea.
Family	I.	Pelecanidæ.
	II.	Pelagornithidæ.
	III.	Phalacrocoracidæ.
	IV.	Odontopterygidæ.
	V.	Anhingidæ.
	VI.	Sulidæ.
Superfamily	II.	Phaëthonitoidea.
Family	I.	Phaëthontidæ.
Superfamily	III.	Fregatoidea.
Family	I.	Fregatidæ.
Supersuborder	VIII.	ICHTHYORNITHIFORMES.
Suborder	XII.	ICHTHYORNITHES.
Family	I.	Ichthyornithidæ.
	II.	Apatornithidæ.
Supersuborder	IX.	LARIFORMES.
Suborder	XIII.	LONGIPENNES.
Family	I.	Rhynchopidæ.
	II.	Stercorariidæ.
	III.	Laridæ.

Suborder	XIV.	ALCÆ.
Family	I.	Alcidæ.
Suborder	XV.	CHIONIDES.
Family	I.	Chionididæ.
Supersuborder	X.	CHARADRIIFORMES.
Suborder	XVI.	LIMICOLÆ.
Family	I.	Charadriidæ.
	II.	Arenariidæ.
	III.	Hæmatopodidæ.
	IV.	Aphrizidæ.
	V.	Scolopacidæ.
	VI.	Phalaropodidæ.
	VII.	Recurvirostridæ.
Superfamily	I.	Jacanoidea.
Family	I.	Jacanidæ.
Suborder	XVII.	CURSORÆ.
Family	I.	Thinocoridæ.
	II.	Dromadidæ.
	III.	Glareolidæ.
	IV.	Cursoriidæ.
Superfamily	II.	Otidoidea.
Family	I.	Œdicnemidæ.
	II.	Otididæ.
Supersuborder	XI.	STEREORNITHIFORMES.
Suborder	XVIII.	STEREORNITHES.
Family	I.	Phororhacidæ.
Supersuborder	XII.	GRUIFORMES.
Suborder	XIX.	GRUES.
Superfamily	I.	Gruioidea.
Family	I.	Gruidea.
	II.	Psophiidæ.
Superfamily	II.	Cariamoidea.
Family	I.	Cariamidæ.
Superfamily	III.	Eurypgoidæ.
Family	I.	Eurypygidæ.
	II.	Rhinochetidæ.
	III.	Mesitidæ.
	IV.	Aptornithidæ.

Supersuborder	XIII.	Ralliformes.
Suborder	XX.	Fulicariæ.
Superfamily	I.	Heliornithoidea.
Family	I.	Heliornithidæ.
Superfamily	II.	Ralloidea.
Family	I.	Rallidæ.
	II.	Aramidæ.
Supersuborder	XIV.	Apterygiformes.
Suborder	XXI.	Apteryges.
Family	I.	Apterygidæ.
Supersuborder	XV.	Galliformes.
Suborder	XXII.	Hemipodi.
Family	I.	Hemipodidæ.
Suborder	XXIII.	Crypturi.
Family	I.	Crypturidæ.
Suborder	XXIV.	Gallinæ.
Family	I.	Megapodidæ.
	II.	Cracidæ.
	III.	Phasianidæ.
	IV.	Tetraonidæ.
	V.	Odontophoridæ.
	VI.	Numididæ.
	VII.	Meleagridæ.
Suborder	XXV.	Opisthocomi.
Family	I.	Opisthocomidæ.
Supersuborder	XVI.	Pteroclidiformes.
Suborder	XXVI.	Pterocletes.
Family	I.	Pteroclididæ.
Supersuborder	XVII.	Columbiformes.
Suborder	XXVII.	Columbæ.
Family	I.	Treronidæ.
	II.	Columbidæ.
	III.	Peristeridæ.
	IV.	Gouridæ.
	V.	Didunculidæ.
Suborder	XXVIII.	Didi.
Family	I.	Dididæ.
Supersuborder	XVIII.	Palamedeiformes.

Suborder	XXIX.	PALAMEDEÆ.
Family	I.	Palamedeidæ.
Supersuborder	XIX.	ANSERIFORMES.
Suborder	XXX.	ANSERES.
Family	I.	Gastornithidæ.
	II.	Anatidæ.
Supersuborder	XX	PHŒNICOPTERIFORMES.
Suborder	XXXI.	PHŒNICOPTERI.
Family	I.	Palæolodidæ.
	II.	Phœnicopteridæ.
Supersuborder	XXI.	PELARGIFORMES.
Suborder	XXXII.	HERODIONES.
Family	I.	Ibididæ.
	II.	Plataleidæ.
	III.	Ciconiidæ.
	IV.	Scopidæ.
	V.	Ardeidæ.
	VI.	Balænicipitidæ.
Supersuborder	XXII.	ACCIPITRIFORMES.
Suborder	XXXIII.	ACCIPITRES.
Superfamily	I.	Falconoidea.
Family	I.	Serpentariidæ.
	II.	Falconidæ.
	III.	Milvidæ.
	IV.	Pandionidæ.
	V.	Vulturidæ.
Superfamily	II.	Cathartoidea.
Family	I.	Cathartidæ.
Supersuborder	XXIII.	PSITTACIFORMES.
Suborder	XXXIV.	PSITTACI.
Superfamily	I.	Psittacoidea.
Family	I.	Nestoridæ.
	II.	Loriidæ.
	III.	Cyclopsittacidæ.
	IV.	Cacatuidæ.
	V.	Psittacidæ.
Superfamily	II.	Stringopoidea.
Family	I.	Stringopidæ.

Supersuborder	XXIV.	STRIGIFORMES.
Suborder	XXXV.	STRIGES.
Family	I.	Bubonidæ.
	II.	Strigidæ.
Supersuborder	XXV.	CAPRIMULGIFORMES.
Suborder	XXXVI.	STEATORNITHES.
Family	I.	Steatornithidæ.
Suborder	XXXVII.	PODARGI.
Family	I.	Podargidæ.
Suborder	XXXVIII.	CAPRIMULGI.
Family	I.	Caprimulgidæ.
Supersuborder	XXVI.	CORACIIFORMES.
Suborder	XXXIX.	LEPTOSOMATI.
Family	I.	Leptosomatidæ.
Suborder	XL.	CORACIÆ.
Family	I.	Coraciidæ.
Supersuborder	XXVII.	HALCYONIFORMES.
Suborder	XLI.	HALCYONES.
Family	I.	Dacelonidæ.
	II.	Alcedinidæ.
Suborder	XLII.	BUCEROTES.
Family	I.	Bucerotidæ.
Suborder	XLIII.	UPUPÆ.
Family	I.	Upupidæ.
	II.	Irrsoridæ.
Suborder	XLIV.	MEROPES.
Family	I.	Meropidæ.
Suborder	XLV.	MOMOTI.
Family	I.	Momotidæ.
Suborder	XLVI.	TODI.
Family	I.	Todidæ.
Supersuborder	XXVIII.	TROCHILIFORMES.
Suborder	XLVII.	TROCHILI.
Family	I.	Trochilidæ.
Supersuborder	XXIX.	JACAMARIFORMES.
Suborder	XLVIII.	GALBULÆ.
Family	I.	Bucconidæ.
	II.	Galbulidæ.

Supersuborder	XXX.	TROGONIFORMES.
Suborder	XLIX.	TROGONES.
Family	I.	Trogonidæ.
Supersuborder	XXXI.	COCCYGIFORMES.
Suborder	L.	MUSOPHAGI.
Family	I.	Musophagidæ.
Suborder	LI.	COCCYGES.
Family	I.	Cuculidæ.
Supersuborder	XXXII.	COLIFORMES.
Suborder	LII.	PAMPRODACTYLÆ.
Family	I.	Coliidae.
Supersuborder	XXXIII.	PICARIFORMES.
Suborder	LIII.	CAPITONES.
Family	I.	Capitonidæ.
Suborder	LIV.	RHAMPHASTIDES.
Family	I.	Rhamphastidæ.
Suborder	LV.	INDICATORES.
Family	I.	Indicatoridæ.
Supersuborder	XXXIV.	PICIFORMES.
Suborder	LVI.	PICI.
Family	I.	Picidæ.
Supersuborder	XXXV.	CYPSELIFORMES.
Suborder	LVII.	CYPSELI.
Family	I.	Macropterygidæ.
	II.	Cypselidæ.
Supersuborder	XXXVI.	EURYLÆMIFORMES.
Suborder	LVIII.	EURYLÆMI.
Family	I.	Eurylæmidæ.
Supersuborder	XXXVII.	MENURIFORMES.
Suborder	LIX.	MENURI.
Family	I.	Menuridæ.
Supersuborder	XXXVIII.	ATRICHONITHIFORMES.
Suborder	LX.	ATRICHONITHES.
Family	I.	Atrichonithidæ.
Supersuborder	XXXIX.	PASSERIFORMES.
Suborder	LXI.	MESOMYODI.
Family	I.	Pteroptochidæ.
	II.	Conopophagidæ.

	III.	Formicariidæ.
	IV.	Dendrocolapidæ.
	V.	Tyrannidæ.
	VI.	Pipridæ.
	VII.	Cotingidæ.
	VIII.	Phytotomidæ.
	IX.	Pittidæ.
	X.	Philepittidæ.
	XI.	Xenicidæ.
Suborder	LXII.	ACROMYODI.
Family	I.	Hirundinidæ.
	II.	Muscicapidæ.
	III.	Campophagidæ.
	IV.	Pycnonotidæ.
	V.	Timelidæ.
	VI.	Mimidæ.
	VII.	Troglodytidæ.
	VIII.	Cinclidæ.
	IX.	Turdidæ.
	X.	Sylviidæ.
	XI.	Vireonidæ.
	XII.	Ampelidæ.
	XIII.	Prionopidæ.
	XIV.	Lanidæ.
	XV.	Sittidæ.
	XVI.	Paridæ.
	XVII.	Zosteropidæ.
	XVIII.	Dicæidæ.
	XIX.	Nectariniidæ.
	XX.	Meliphagidæ.
	XXI.	Certhiidæ.
	XXII.	Mniotiltidæ.
	XXIII.	Motacillidæ.
	XXIV.	Alaudidæ.
	XXV.	Fringillidæ.
	XXVI.	Drepanidæ.
	XXVII.	Cærebidæ.
	XXVIII.	Tanagridæ.

Family XXIX.	Ploceidæ.
XXX.	Icteridæ
XXXI.	Oriolidæ.
XXXII.	Dicruridæ.
XXXIII.	Eulabetidæ
XXXIV.	Sturnidæ.
XXXV.	Paradiseidæ.
XXXVI.	Corvidæ.

OBSERVATIONS ON HEARING AND SMELL IN SPIDERS.[1]

ANNIE H. PRITCHETT.

Only a small amount of previous work has been done upon the senses of hearing and smell in spiders.

According to Campbell ('80) spiders are well provided with the means of feeling the slightest movements of their webs or other near objects. On their legs are long, slender, silken hairs which differ from other hairs in that they are attached to a disc on the integument.

Dahl ('83) found these hairs to vibrate to the tones of a violin and designated them as auditory hairs. Later ('84) he distinguished certain of these as organs of smell and attempted a classification of spiders according to the distribution of the various hairs.

Bertkau ('85) compared the so-called taste organs on the ends of the palps with the flask-shaped bodies on the antennæ of ants and spoke of them as organs of smell.

J. W. and E. S. Peckham ('87) found that with three exceptions all the spiders experimented upon by them gave responses to strong smelling substances, but the Epeiridæ alone seemed capable of hearing the vibrations of a tuning fork. Orb-making spiders were the most sensitive to these vibrations, while those that make no web gave not the slightest heed to the sounds, and in the former the sense seemed to be distributed generally over the whole epidermis.

Wagner ('88) insisted that the so-called auditory hairs are only capable of perceiving tactile sensations.

Gaubert ('90) considered the lyriform organs as organs of hearing.

[1] Contributions from the Zoölogical Laboratory of the University of Texas, No. 59. A thesis submitted to the Faculty of the Department of Literature, Science and Arts of the University of Texas for the degree of Master of Science.

McCook ('90) concludes that the senses of smell and hearing are very rudimentary and are distributed over the entire body. They are located in the delicate hairs which constitute the covering and armature, so that the nervous system receives through these organs or appendages impressions that may be considered analogous to hearing and smell in the higher animals. Further, the sense of hearing can scarcely be distinguished from that of touch as it is known to us. He thinks that even in the orb-weavers there is no true sense of hearing, but that the web filaments transmit the vibrations and the sensation is tactile rather than auditory.

Pocock ('93) found spiders sensitive to heat, provided with acute sense of taste, with defective sight and no hearing whatever.

Dahl (:04) designates the auditory hairs as trichobothria and makes an elaborate classification of suborders according to their distribution.

The two species used by me for experiment are *Geolycosa texana* Montg. and *Pardosa mercurialis* Montg. and are found in great abundance in Austin, Texas, and its vicinity. The large *Geolycosa texana* lives in underground holes of $\frac{1}{2}$ to $1\frac{1}{2}$ inches in diameter and digs its home on creek banks or in the fields wherever the ground is comparatively clear except for a close sod of native grass. *Pardosa mercurialis* has been found mainly under small surface stones along the banks of streams or in the dry beds during droughts, but sometimes occurs in great abundance far from water.

The specimens used for the observations were kept in cages made by fastening glass plates together at their edges with gummed linen, as described by Montgomery (:03).

1. Experiments on Hearing.

The apparatus used for these experiments were tuning forks of 128, 256, 320, 384 and 512 vibrations and a specially prepared, isolated cage. The cage was made of three glass plates fastened with gummed linen and covered with black paper,

except on the bottom. A small hole was left in the paper of one side to admit light and one in the top for observations. The bottom was of mosquito netting which served to admit the sound waves from below. The cage, supported at the three corners by wooden posts 10 *cm.* high, rested on a wooden float, the float in a stone jar filled with water and attached to it by rubber bands. A layer of sawdust three inches thick isolated the jar and stool upon which it stood from vibrations from without. The apparatus, though placed in a quiet, darkened corner of the laboratory, was used only when there were as few outside disturbances as possible.

a. Geolycosa texana Montg.

♀ No. 13 was placed in the hearing cage and left unmolested one hour. At the end of that time successive trials were made with tuning forks of 128, 256, 320 and 512 vibrations, but no response whatever was obtained. At two later dates the experiments were repeated but with no more definite results. The same results were obtained with three other females, in each case using all the tuning forks. Also a male, after remaining quiet one hour in the hearing cage was tested with all the forks but gave no response.

b. Pardosa mercurialis Montg.

♀ No. 5 was placed in the hearing cage and after an hour's intermission was tested with the forks but remained perfectly quiet. She was left in the cage over night and tested next morning but gave no response.

♀ No. 6 was tested by three separate series of experiments, the first after two intervals of an hour and the third after a half hour had elapsed, but she did not respond to any of the sounds. During the first series she cleaned her palps and legs in the normal way as if nothing unusual were happening. No responses were obtained on similar experiments with two other females and a male.

At another time a steel bar which gave a pitch of approxi-

mately 2300 vibrations was suspended above the hearing cage and struck repeatedly with a metal hammer. Eight fresh specimens were placed successively in the cage but no spider made any motion that could be interpreted as a response to the sound.

Again, a mason's trowel was held near the cage and struck several times with a metal bar producing a loud, crashing noise, but the spiders made no motion whatever.

2. Experiments on Smell.

These experiments were undertaken to ascertain first whether the spiders possessed the sense of smell and second to localize the same, if possible, in case it was found to exist. The experiments were made mostly upon *Pardosa mercurialis.*

Two classes of the essential oils were used as tests. Those of the first class were the non-irritants, lavender, cedar, wintergreen, almond, juniper-berries, bergamot, cassia and cloves; of the second class, those irritants that will cause sneezing in man were oils of mustard and black pepper. The results from the use of the two irritating oils were essentially the same as those for the stronger oils of the non-irritating class, and the reactions were the same in every case only that they were more intensified with the oils of stronger odors.

The hearing cage was used for the smell experiments.

Small glass rods were dipped into the oil and the drop that adhered was held immediately below the cage. In each case the spider seemed repelled to a greater or less degree corresponding to the strength of the oil, and in no instance was it attracted toward the stimulus. The males and females gave exactly the same response, thus showing that neither sex has a superior sense of smell.

The responses were (1) turning away and moving as far as possible from the odor, (2) vibratory movements of the palps and mandibles, (3) raising each leg as the oil is applied beneath it. In some cases all the responses were given to a single stimulus, in others only one, or a combination of either two.

Experiments were made first on unmutilated specimens to

ascertain the normal reaction to odors, then upon individuals variously mutilated in order to localize the olfactory sense.

a. Observations on Unmutilated Individuals.

Lavender.— Tests were made with eight females and seven males and each responded by running from the stimulus. In four cases this was accompanied by motions of the palps and mandibles.

Wintergreen. — Seven females and four males. In five cases the palps gave definite vibratory responses and in the others the spiders turned away.

Bergamot. — Six males and six females. Each time the spiders turned away, and in seven instances responded with motions of the palps.

Cassia. — Six males and six females. All but one turned quickly away, and eight gave vibratory motions of the palps.

Clove. — Six females and five males. One female gave no response, six gave movements of palps and mandibles, while ten responded also by turning away.

Cedar. — Eight females and six males. The responses were quite indefinite, palpal vibration in two cases, and in four there was no motion whatever.

Almond.— Seven females. No palpal movements were given and the spiders turned away indifferently.

Juniper-berries. — Eight females and six males. The responses were quite slow and consisted generally in turning away. The palps were moved slightly but not in a vibratory manner.

Mustard.— Six males and eight females. The responses were no more decided than those given to strong oils of the non-irritating class. In only one instance were there definite palpal movements, and the spiders usually turned quickly away at first, then later more slowly, as if overcome by the odor.

Black pepper. — Six males and six females. The responses were quite slow and given after prolonged stimulation. Vibratory motions of the palps were entirely lacking.

b. Observations on Individuals with Palps extracted.

It next seemed desirable to determine the location of the olfactory sense, and for this purpose the oils that produce definite results with the unmutilated individuals were used exclusively.

Both palps were extracted with forceps at the femoro-trochanteral joint from twelve females and six males, and after a week had elapsed experiments were made with three non-irritating oils, lavender, wintergreen and bergamot.

Lavender.— In every case the spider gave definite responses to the stimulus. When the drop of oil was held directly beneath each leg successively, each responded by a slight, quick, upward jerk. Almost without exception the first pair were raised highest and held poised in the air several moments or until the other legs were stimulated. The second pair were not raised so high as the first, nor the third pair so high as the second, and rarely ever both at the same time. The fourth pair were usually raised only a little distance and then drawn up closer to the body while the spider moved away.

Wintergreen. — The same specimens, twelve females and six males, were used and practically the same results were obtained.

Bergamot.— A similar series of experiments was performed on the twelve females and responses corresponding to the above were given, though bergamot appears to offer a weaker stimulus than the other two oils used.

Cassia.— The palps were extracted from twelve other males and six other females and experiments were performed after twenty-four hours. In only one instance did the spider fail to respond, all others showing the usual reactions — the first pair of legs responding most definitely and the others less so. The spiders usually turned away after a few applications of the stimulus.

c. Observations with the First Pair of Legs Removed.

In five females and six males the palps were left intact but the first pair of legs were similarly removed with forceps. The

responses were exactly the same as in the foregoing series Thus it was shown that the sense of smell is not localized in the palps nor in any one pair of legs, but that each is capable of perceiving the stimulus to a certain degree and of giving a definite response to it.

d. Observations on Individuals with the Sense Hairs removed.

The theory has several times been advanced that the long, spiny hairs on the legs of these spiders are organs of special senses, accordingly all these hairs were cut off the tarsi and tibia of male No. 94 and after twenty-one hours it was tested with lavender oil. Each leg responded as do those from which no spines were removed.

Female No. 95 had the hairs cut from the entire leg and each leg sand-papered, still it gave the normal response to bergamot twenty-one hours after the operation.

Female No. 96 had all the legs sandpapered, yet after only an hour's time it responded normally to bergamot, raising each leg in succession.

Male No. 97 had the tarsus of each leg removed and the spider seemed to suffer more than when an entire leg was cut off. However after twenty-two hours it responded normally to bergamot, raising each leg as it was stimulated. It was not considered safe to cut the legs at any higher joint, but the experiments seem to indicate that the entire leg possesses the ability to perceive sensations of odors.

3. Conclusions.

1. Neither Geolycosa nor Pardosa respond to tuning forks of 128, 256, 320, 384 and 512 vibrations. No responses were given to a metal bar of approximately 2300 vibrations nor to the crashing sound of a metal plate when struck with a bar. Therefore it is quite probable that these spiders do not hear at all.

2. It might be supposed that possibly this extreme quiescence was itself an indication that the spiders perceived the tones and responded in this way; however the fact that these spiders

remain motionless in their cages for hours together seems to prove that the sound is not perceived in any measure, or at least that it produces no response. All parts of the body are extremely sensitive to touch and the spider responds immediately if it or the cage comes in contact with the vibrating tuning fork.

3. Males and females respond exactly alike to stimuli of smell and hearing.

4. Pardosa responds normally to the essential oils by turning away, making vibratory movements with palpa and mandibles, and raising each leg as it is stimulated.

5. Individuals from which the palps have been removed respond to odors normally with each leg.

6. Individuals with the first pair of legs removed respond normally with the palps and the remaining three pairs of legs.

7. Spiders that have had the sense hairs cut off or sand-papered respond as do normal specimens.

8. Specimens with the tarsal joint cut from each leg respond as usual by raising each leg when stimulated.

9. From the foregoing results it seems quite evident that the ability to perceive odors is distributed over the whole integument of the spider and there is no definitely localized olfactory organ.

The work for this paper has been done entirely under the direction of Dr. T. H. Montgomery, Jr., and the writer is indebted to him for many valuable suggestions as well as sympathetic interest and encouragement.

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AMITOSIS IN THE EMBRYO OF FASCIOLARIA.

HENRY LESLIE OSBORN.

A NUMBER of years ago, while studying the embryology of Fasciolaria, I noticed evidences of amitosis in three different locations. As biological opinion has not reached a state of rest in regard to amitosis and its relation to mitosis, I have felt that a study of the facts in this case would perhaps prove of interest. A few brief references to the literature of the subject will show the unsettled condition of public opinion in this matter. Waldeyer ('90) said that "nuclear division is a single process with Remak's simple amitotic division as the fundamental form." Johnson ('92), on the contrary, said that he was "convinced that it (amitosis) is not derived from mitosis, and on the other hand is not a forerunner of the more complicated process." Johnson considers it a different type which along with karyokinesis has been transmitted from the simplest forms of life to the most highly organized. Nor is there unanimous consent as to the significance of amitosis. The bulk of observation is to the effect that mitosis is found in growing (*i. e.*, regenerative) tissue and amitosis is found in senescent, metabolic or pathologic tissue. In 1891 Ziegler contended that amitosis is due to senescence or highly active secretory action in cells, and vom. Rath ('94) espoused this view and defended it strongly. According to these writers amitosis is never regenerative (*i. e.*, found in developing tissue), but seals the fate of a nucleus which can never subsequently divide mitotically. E. B. Wilson in his work, *The Cell*, appears to be less favorably disposed to accept this view in the 1900 edition of his work than in the edition of 1896; in the 1900 edition he says that the view is "too extreme," though "there can be no doubt but that Flemming's hypothesis in a general way represents the truth, and that in the vast majority of cases amitosis is a secondary process which does not fail in the generative series of cell-divisions."

Some observations exceptional to this law may be briefly cited. Frenzel ('85) found in the intestine of certain decapods that the epithelium is regenerated from basal cells which show all stages of amitosis, while in other closely related genera the growth is from mitotic nuclei. Wheeler ('89) found that in the early blastoderm of Blatta all the nuclei divide amitotically at a certain stage, and that this is followed later by mitosis. Goppert ('91) found amitosis in the leucocytes of the salamander's liver which he regards as regenerative. Verson ('91) found that in the testis of the silkworm single large nuclei divide amitotically while their daughter cells give rise to spermatocytes mitotically. Meves ('91) found that in the salamander certain of the cells of the testis divided amitotically in winter and mitotically in summer. Preusse ('95) found mitosis in the youngest egg compartments of the ovaries of hemiptera, which consist of only a few cells and where active cell multiplication must be taking place. This writer cites observations of Carnoy and Claus in support of his claim that amitosis is regenerative in some cases. Pfeffer ('99, Wilson, :00) found that if "spirogyra be placed in water containing 0.5–1.00% of ether active growth and division continue, but only by amitosis. If, however, the same individuals be replaced in water mitotic division is resumed and an entirely normal growth continues."

These various observations upon amitosis all indicate a close relation between amitosis and mitosis. The fact that nuclei divide in one way in winter and in the other in summer, that in one genus one method prevails and in another related genus the other, and that mitosis can be replaced in the same cell by amitosis under the influence of ether, all of them suggest a process at bottom the same but operating differently under the influence of different circumstances. If so, we should regard amitosis as the more primitive mode and mitosis as a more highly specialized mode derived from it. And we need not then be surprised if the more primitive mode should occasionally occur in a place where on general principles we should look for the more highly specialized one. Though we generally find cell multiplication to be associated with mitosis and special metabolic activity to be associated with amitosis, we might in special cases find that cells

were multiplying by amitosis, the simpler mode having been adopted for local reasons.

The material on which this paper is based was collected at Beaufort, North Carolina (Osborn, '85), and preserved in either cold aqueous corrosive sublimate, picronitric or chromic acid solution. Sections were cut serially and stained on the slide in borax-carmine, in the days before iron-hæmatoxylin had been

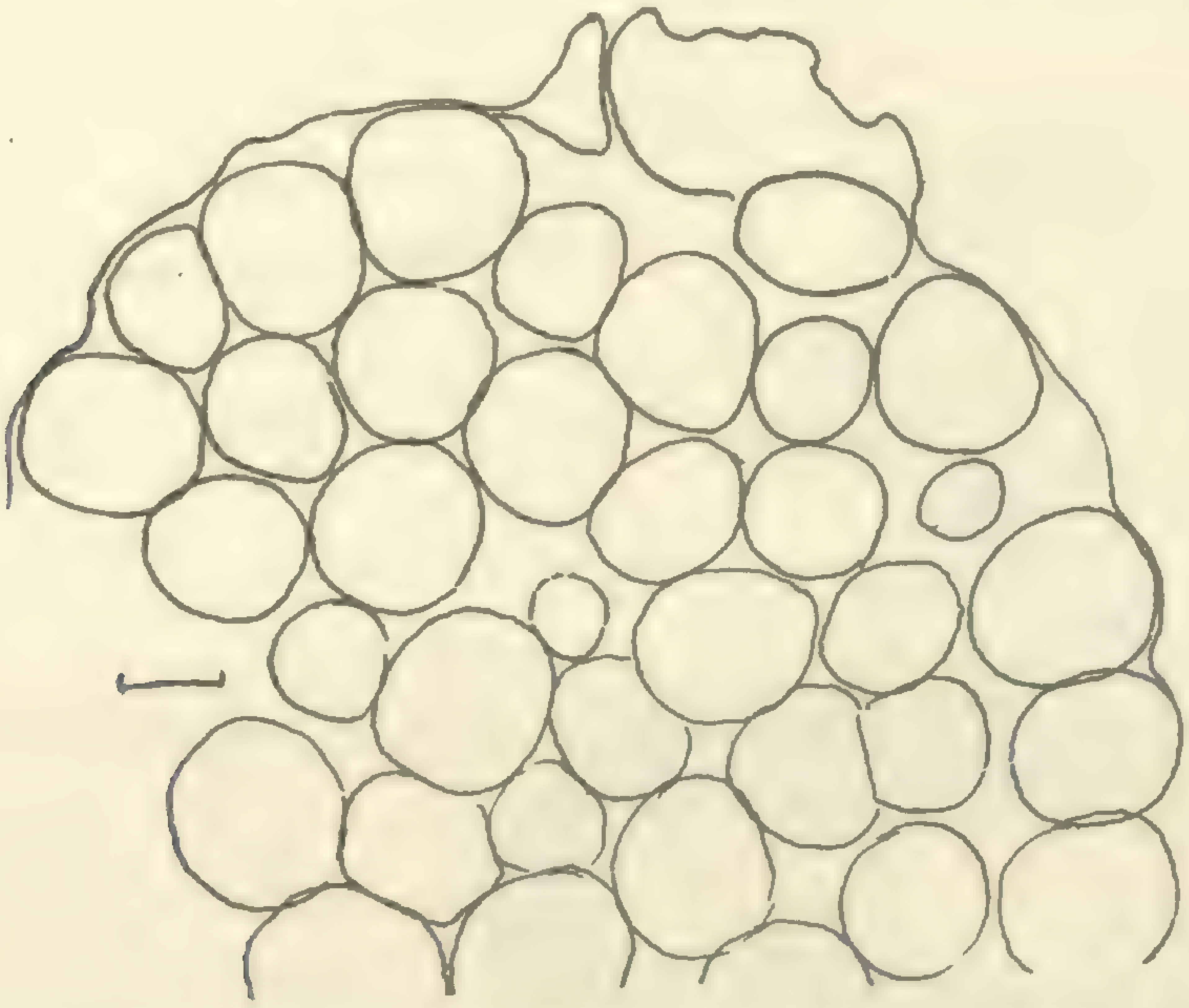

FIG. 1.—Section of embryo in plane of the throat, showing the very thin ectoderm, partial endoderm and food-ova. Scale 0.1 mm., cam. luc. × 60.

discovered. I should have been glad to check these results by more recent methods had access to fresh material been possible; however, the technique is fairly adequate for my purpose, as shown by the condition of the mitotic nuclei present and many other delicate cytological details. A brief account of the structure of the embryo will facilitate orientation, especially as this form is considerably aberrant. My studies at Beaufort were broken off before I had gotten the earliest stages. Sections of my earliest embryo are shown in Figs. 1 and 2. It is already past the gastrula stage, and consists of an extremely attenuated ectoderm enclosing a great number of small spherules each of approximately 0.15 mm. in diameter. There is a throat and a small amount of ectoderm, not nearly enough to enclose the spherules. The spherules are made up of a small mass of cyto-

plasm and a great many yolk granules enclosed by a sharp cell wall. In the centre of the cytoplasm there is a nucleus or more than one. These structures are not the ordinary yolk cells resulting from segmentation of the endodermal part of the original ovum, but according to MacMurrich ('87) they are unfertilized ova which were discharged into the egg capsule by the mother at the time of its formation together with the true eggs. He says "each egg capsule contains a large number, perhaps two hundred, of ova measuring about 0.25 mm. across; of these

FIG. 2. — More highly magnified view of part of figure 1, scale 0.1 mm., cam. luc. × .30.

only four or six ever develop, the rest being swallowed by the developing embryos and used as food. The non-developing ova do not ever segment nor push out polar globules, nor do they break down or disintegrate, but are ingested by the embryos so that at an early stage one of these appears to consist of a large number of ova bound together into a ball." The embryo of Fasciolaria is thus very unlike that of related prosobranchs such as Nassa, in which the yolk is a part of the original structure of the egg cell, and hence part of the endoderm of the embryo, while in Fasciolaria the egg segments and reaches the gastrula stage and then swallows the other eggs itself having no supply of food. The ova thus swallowed I shall call food ova.

The larval kidneys are conspicuous organs in many proso-

branch embryos, but they do not reach such large dimensions or become such conspicuous objects in any other described forms as in Fasciolaria. They are called "sub-velar masses" in my paper of '85, and are shown in Figs. 1, 2, 3, 4, and 5. They are very early of development and are already conspicuous organs when the shell gland first shows. The velum subsequently arises and spreads out over them. In the earliest embryos the ectoderm cells of the area on each side of the mouth undergoes a peculiar change (Fig. 3), the boundaries of the cells cannot be seen, vacuoles of various sizes appear in the cytoplasm, and some of the larger vacuoles push the nuclei aside compressing the nucleus, much as in the fat cells of vertebrates. This is the first step in the development of the larval kidney. The nuclei at this time still show mitosis, two of the cells of the figure are in stages of active karyokinesis, there is no evidence as yet of amitosis. As the accumulation of material within the cell goes on, the outer end is pushed up above the general level of the ectoderm and becomes the swollen organ we see. The cells become wedge-shaped, each retains its place on the ectoderm by its base, the cytoplasm is pushed out into the outer end of the cell, which becomes rounded there as if through the influence of pressure from within. The content of the cell is chiefly a material which in life is fluid and highly refractive, but it is coagulated by preservative reagents; it is faintly stainable and not dissolved by absolute alcohol or oil. The cytoplasm at the outer end of the cell (Fig. 4) contains one or more nuclei. The relation of the cells to the general ectoderm is shown in Fig. 4; the organ is considerably constricted at its base.

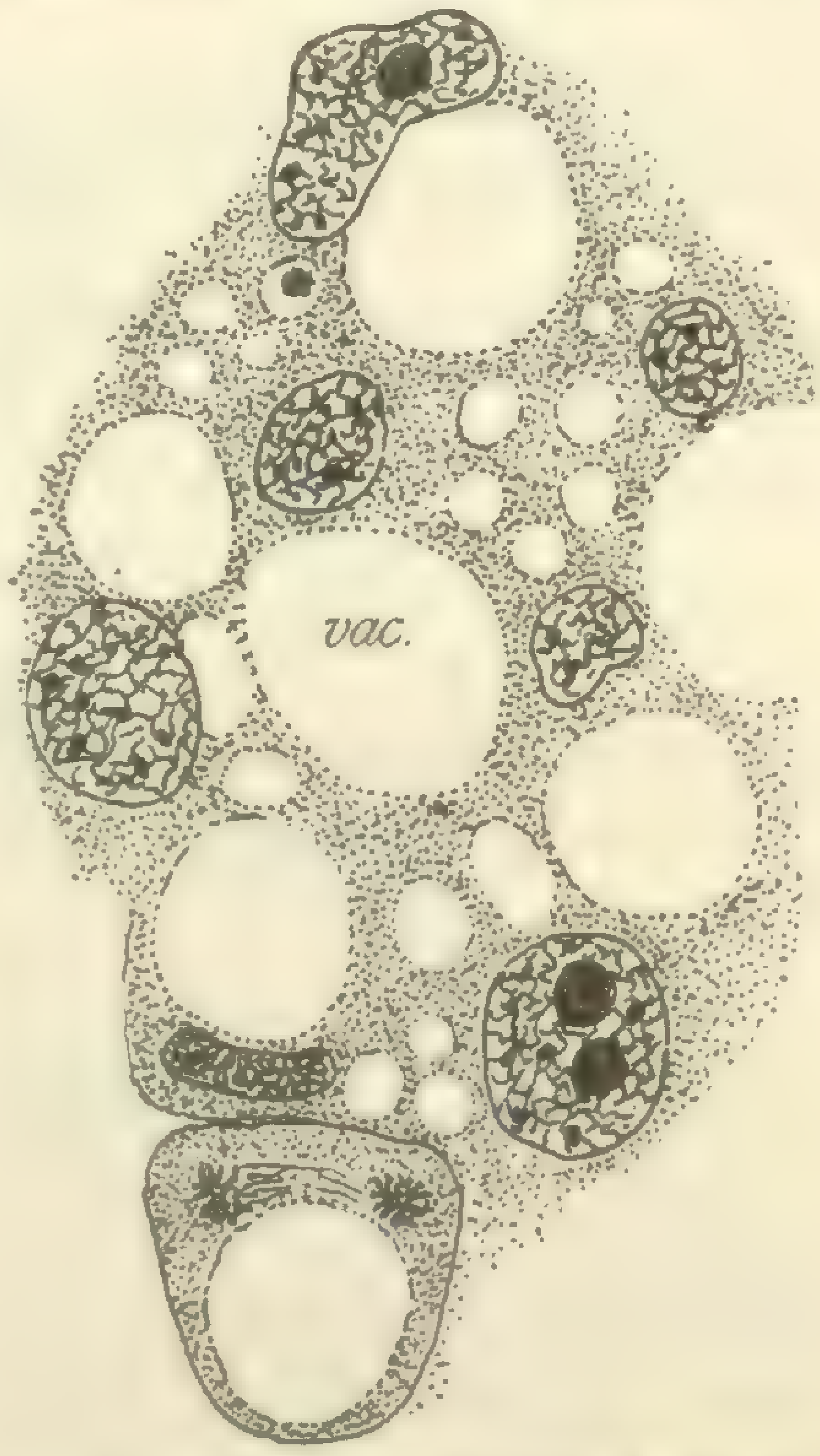

FIG. 3.—Surface view (tangential section) of ectoderm at one side of the mouth, showing first stages in the formation of the larval kidney.

There are no evidences of cell division among the older cells;

additions are evidently made at the periphery of the organ at the expense of the ordinary ectoderm cells. But though the older cells are not dividing, there are many of them in which the cytoplasm at the outer end contains two nuclei, so that we infer that nuclear division has been going on. No mitotic figures are to be found in these cells but there are evidences of amitosis. Fig.

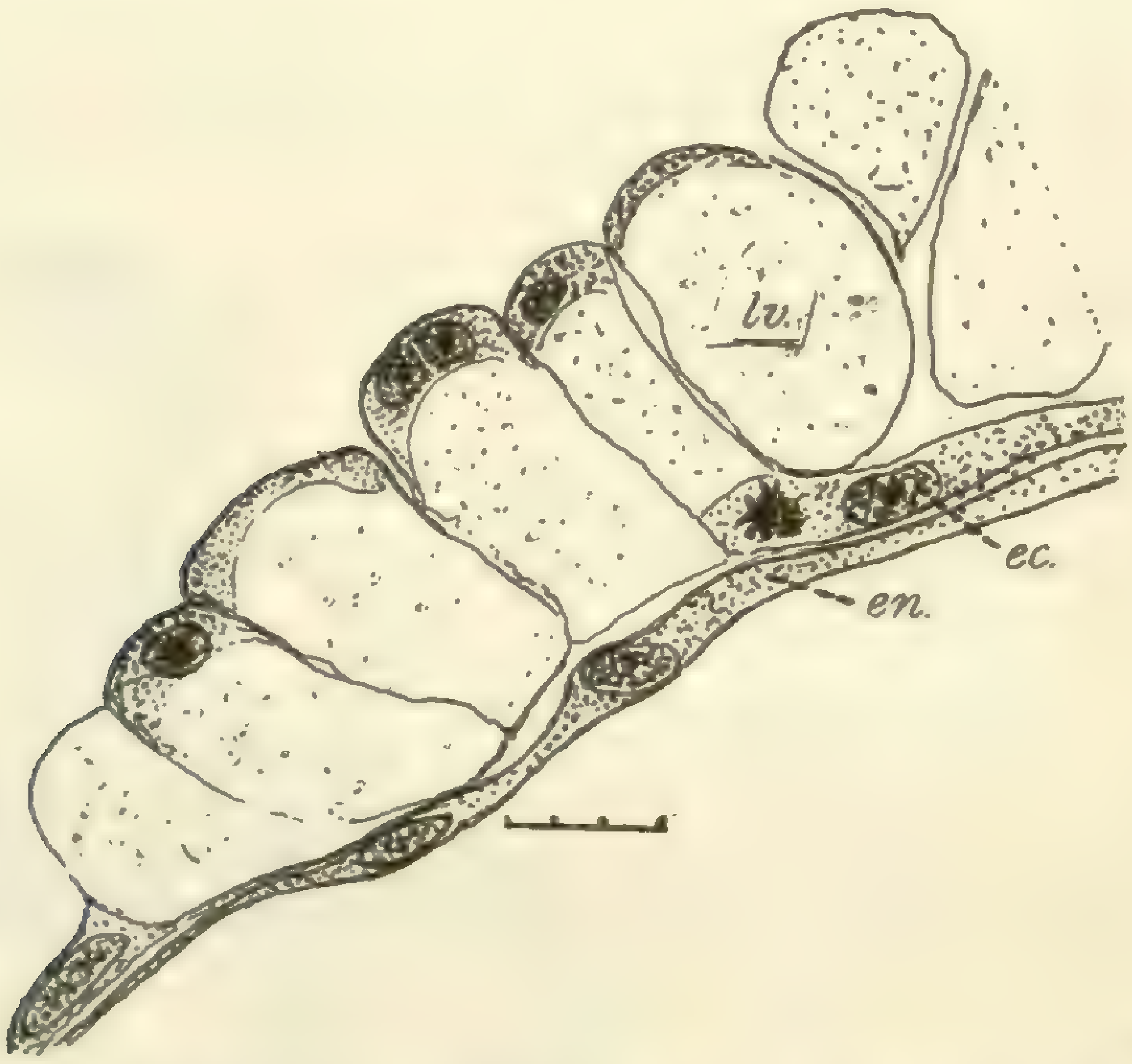

Fig. 4.—Section of the larval kidney at a later stage than figure 3, showing the ectodermal cells greatly enlarged by the secreted material, and the cytoplasm occupying the outer end of the cell, cam. luc. × 211. Scale = .01 mm.

5 shows three stages of this: in the lower figure the initial constriction, in the middle one the completion of the division, and in the upper one the two nuclei have moved apart.

The physiological significance of this organ is indicated by its name. As usual with prosobranchs, the embryo develops inside an impervious capsule; consequently it is of great importance that the wastes from its actively developing tissues be kept out of contact with them. This is done by intracellular storage. The barrier of living cytoplasm at the outer end of the cell keeps the cell the better from disintegrating there and the contained material from escaping. This device reminds one of the lepidoptera and their scales as reservoirs for waste nitrogen during metamorphosis.

Amitosis here is clearly in accordance with the view that senescence and amitosis are closely related, for these cells are

plainly reaching the end of their career. Though they are for the time a part of a very young embryo, the organ is no more an integral part of the embryo than are the embryonic membranes of arachnids and insects, in which amitosis is well known to be associated with senescence. It is really merely an embryonic structure. It is not, however, clear that the active secretory function of these cells is a cause of the amitosis. If it were we should expect that in cells where it was taking place as actively as in the one in Fig. 3 at the bottom of the drawing should show amitosis, whereas it and the one over it are dividing amitotically.

FIG. 5. — Outer ends of three cells from same situation as figure 4, showing nuclei in different stages of division, cam. luc. × 600.

The food-ova present nuclear appearances of sufficient interest to deserve mention. In the earliest embryos (Figs. 1, 2) they are intact and still manifest cell activities of their own notwithstanding their having been swallowed as food. Each has a definite egg-membrane enclosing a mass of cytoplasm often located near the surface of the cell, its branches reaching out among the very numerous grains of yolk. Many of these ova exhibit peculiar nuclear activities. In some one finds a single nucleus near the centre of the cytoplasm of large size and containing within its membrane not the more customary chromatine network but instead a mass of bubbly material (fig. 6) as if the chromatine had been converted into a froth. Other cases are met in which there are numerous small nuclei, as in Fig. 8.

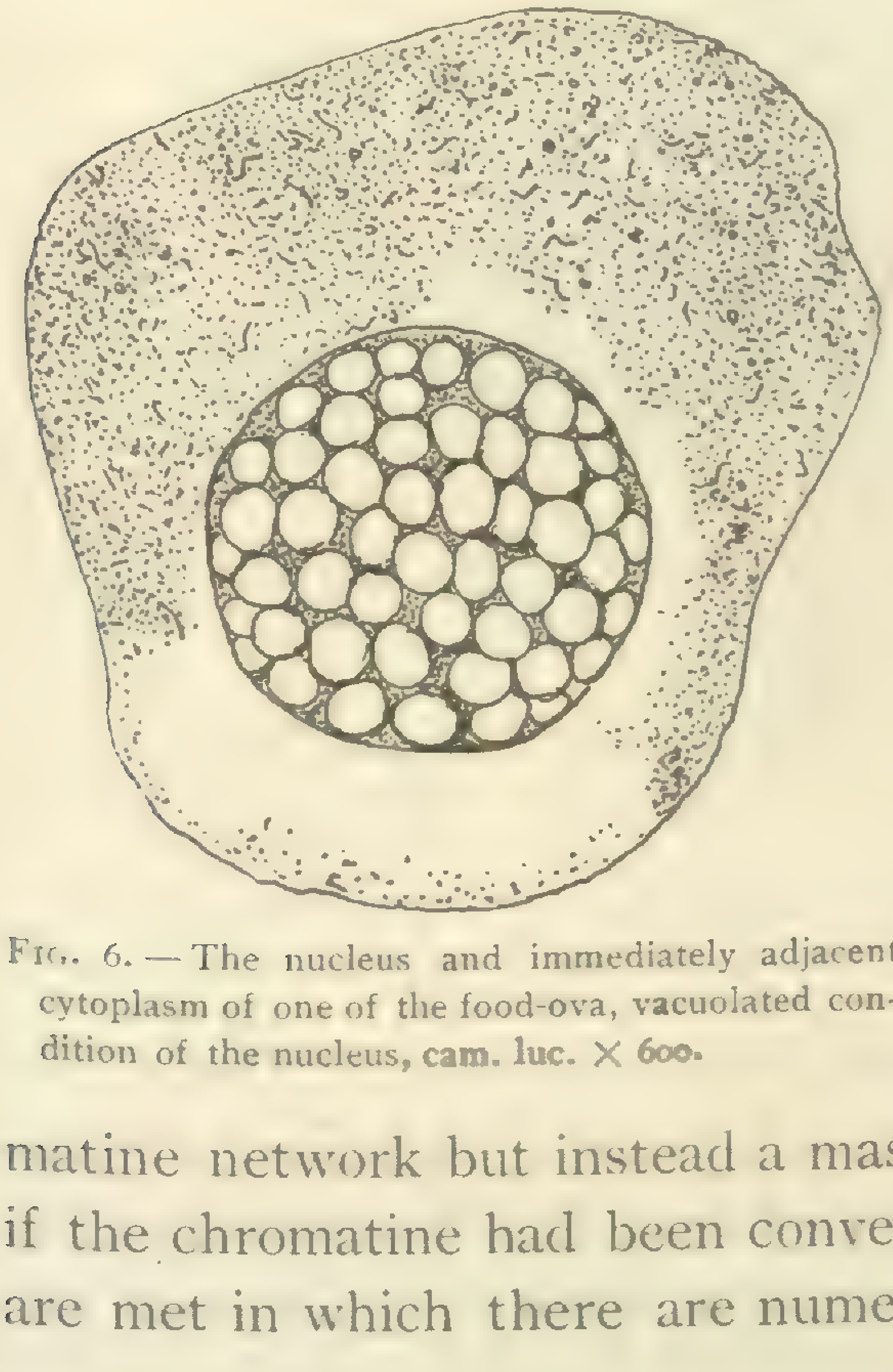

FIG. 6. — The nucleus and immediately adjacent cytoplasm of one of the food-ova, vacuolated condition of the nucleus, cam. luc. × 600.

In such cases the centre of the protoplasmic area often contains a somewhat more deeply stained material not limited by any distinct boundary from the general cytoplasm, but occupying the position of the single nucleus of other ova and having the same size, and the cytoplasm often radiates from this as a centre of influence. The lesser nuclei do not usually show active division, but are in the resting stage. They show evidences of disorganization in various respects. Some are distinctly vacuolated as the parent nucleus was; others contain bits of chromatine of no regular shape or position, resembling very closely the "spore-like bodies" found by Herrick ('92) in the "degenerating nuclei" of the yolk cells of the egg nauplius of Alpheus. In a few instances two of these smaller nuclei are still connected by a thread of stainable material, as in Fig. 7, which I interpret as the last stage in amitotic division, and an indication of the proc-

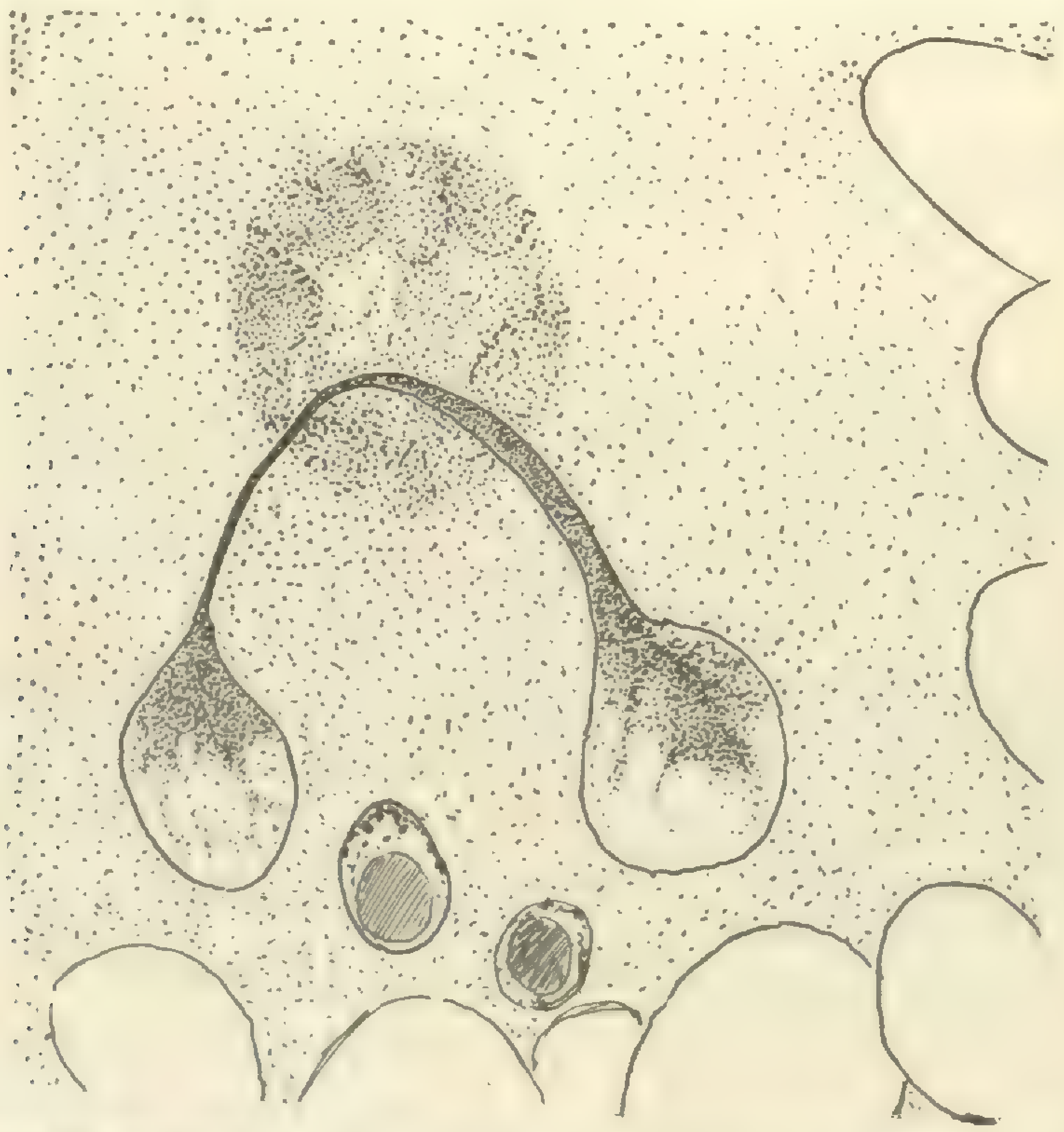

Fig. 7.— Nuclei and surrounding cytoplasm, showing the last stage in a nuclear division, cam. luc. × 600.

ess by which the multiple nuclei of the food-ova have been formed. The cells in which the nuclei have undergone these changes are on the road to complete breakdown and these changes are the last events in their lives. The process is a

futile attempt at segmentation where normally we should find mitosis, but in this case the cell having the impulse to divide but being powerless to do so by mitosis falls back on the easier mode and does so by amitosis. We may call it cell senescence.

The gastrulas before they have swallowed the food-ova are (according to information and drawings access to which I owe to the kindness of Prof. MacMurrich) very queer looking objects on account of the very ample folds of the ectoderm to allow for the distension which is to follow. One would expect that the endoderm would be equally so, in order to receive the ova into an endoderm-lined cavity, but after much study of this point I am convinced that unusual as it is there is not enough endoderm to enclose these ova, but only a very small amount reaching out a short distance from the throat in all directions, as in Fig. 2.

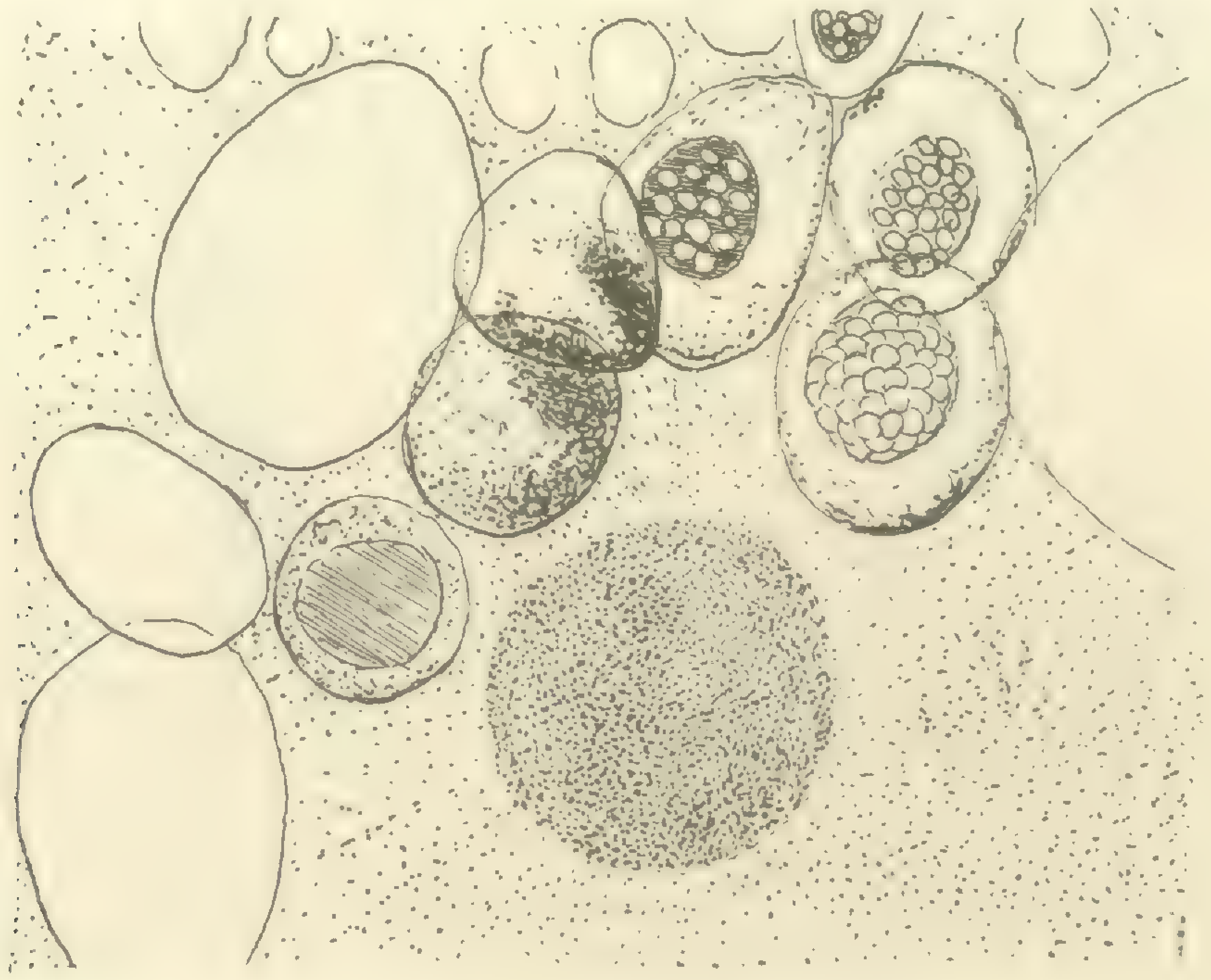

Fig. 8.— Multi-nucleate condition of older food-ovum, the nuclei showing vacuolation, cam. luc. × 600.

A study of various series agrees in showing only one very thin layer the ectoderm in contact with the ova except near the stomodæum. As development progresses the endoderm pushes out around the food-ova, at first with very thin flat cells, which later still become cubical and finally differentiate into the large and vacuolated definitive cells of the liver, or the columnar cells

of the intestine. During the early part of this process, while the endoderm cells are still flat or cubical, and before their final differentiation has taken place, their nuclei exhibit unmistakable evidences of amitosis. Fig. 9 is taken from such an embryo. The food ovum, part of which is shown in the figure, is still intact; it has not yet undergone the breakdown of structure which is soon to take place. The endoderm is composed of

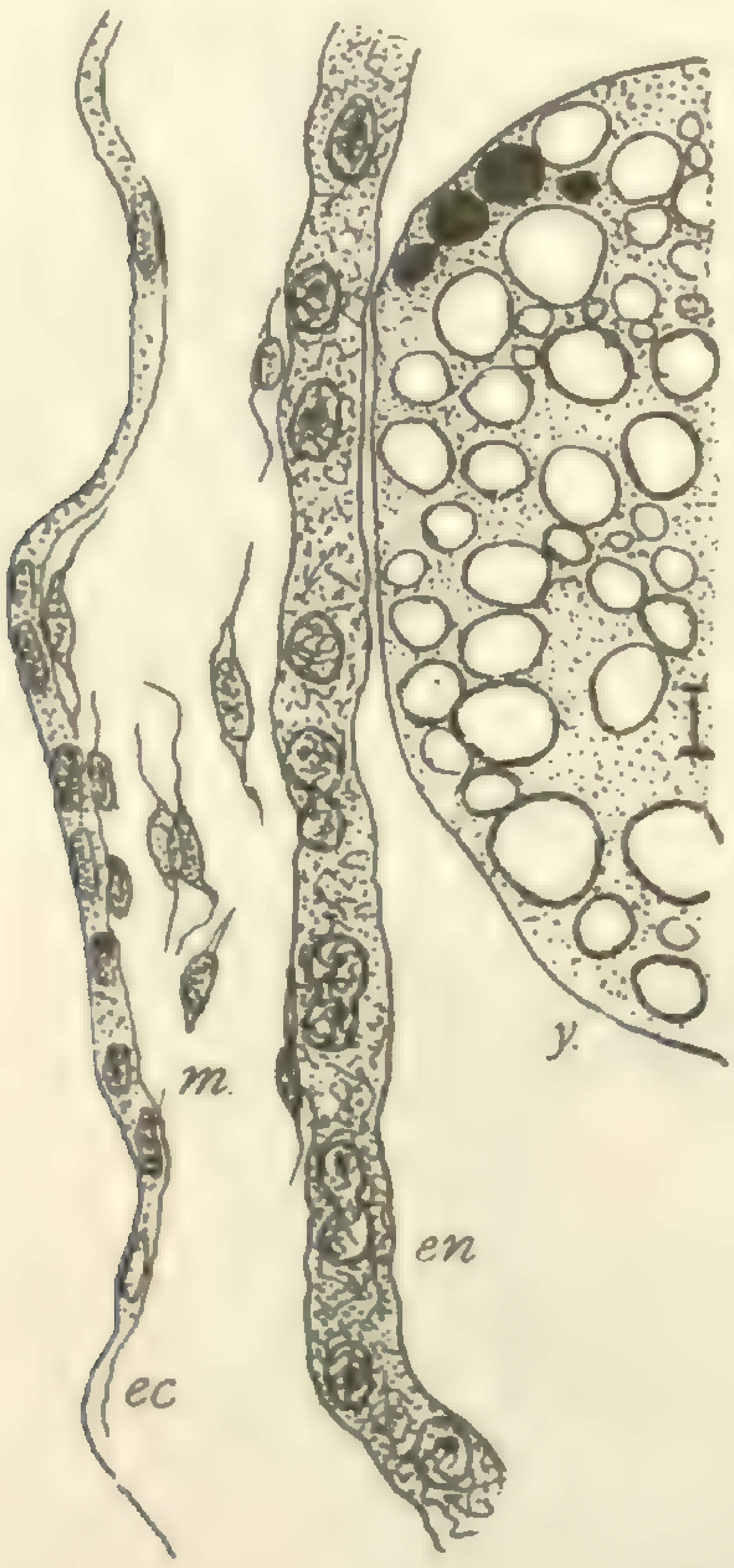

Fig. 9.—Section vertical to the ectoderm and underlying endoderm in very young embryo, scale = .01 mm., cam. luc. × 211.

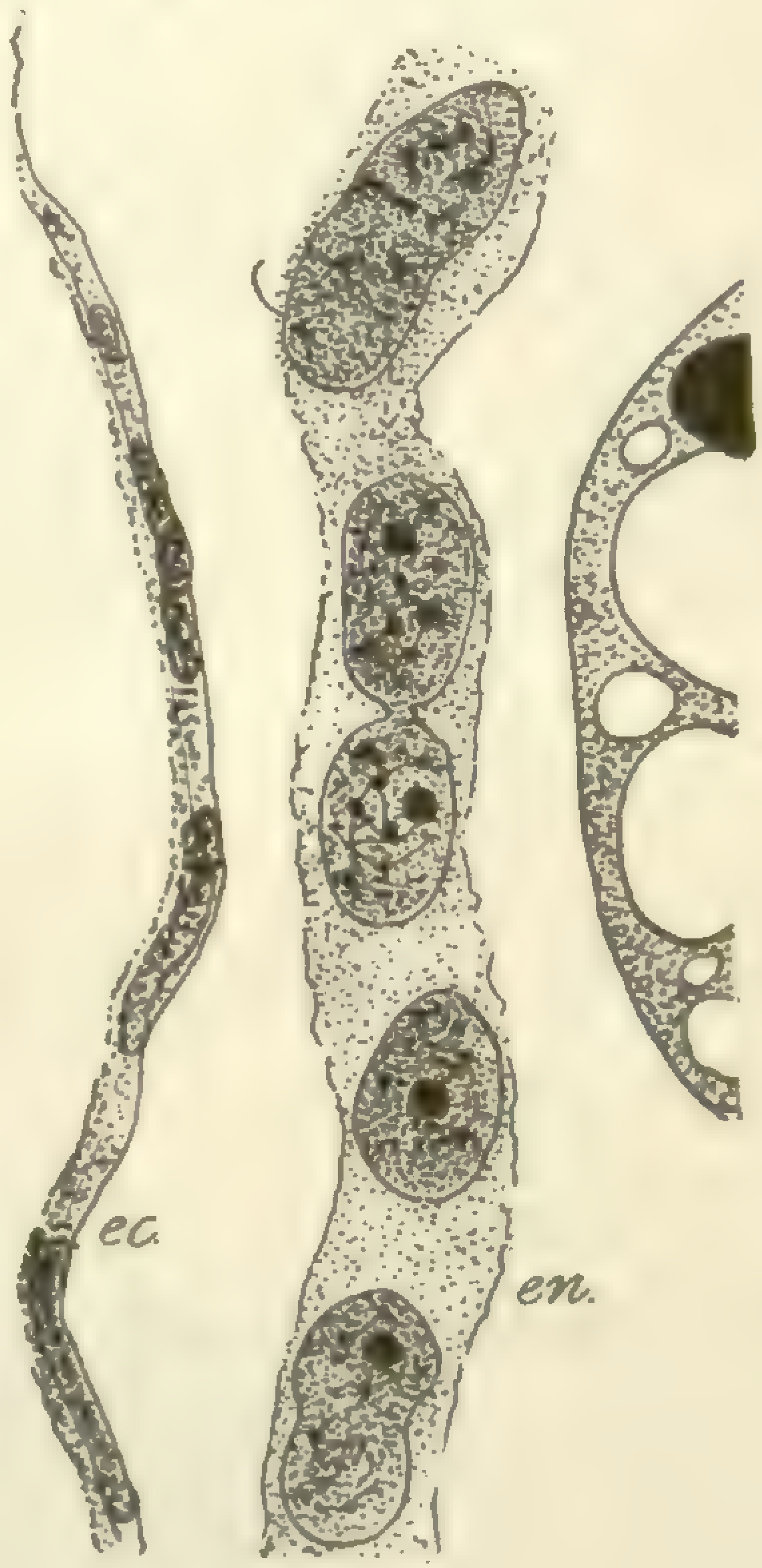

FIG. 10.—More highly magnified view of part of fig. 9, × 600.

cubical cells in which dividing nuclei are to be seen. The endoderm cells do not show any walls at this time between the cells but has the appearance in this view and in surface views of a syncytium. Walls appear at a later date and distinct cells are clearly seen in older embryos. A more highly magnified view of the cells of Fig. 9 (Fig. 10) shows nuclei at different stages of amitotic division. These views are very characteristic and found in many different places in several series of embryos of this age. They are further corroborated by flat views from places where sections are cut tangentially through the endoderm (Fig. 11), in which the syncytial character of the layer is

shown. Large nuclei of irregular shape (Fig. 12) are also found in the endoderm of this stage; they are apparently also forms of amitotic division. Their exact relation to the more typical cases could not be determined from the material which I had. They are quite commonly to be found in embryos of a little older stage but before the endoderm has assumed its definitive form. Nuclei of both these forms predominate decidedly during the development of the embryo, but in addition to them there are occasional nuclei showing unmistakable karyokinetic figures. The latter are too infrequent to be regarded as the nuclei from which the rapidly growing endoderm is being chiefly regenerated, but there is nothing to show that they do not give rise to endoderm cells as well as the amitotic nuclei. The presence of the mitotic figure is a guarantee of the adequacy of the technique, whatever we may think of the amitosis in these cases, at least it is not possible to dispose of them as artifacts. We recall in this connection the cases of amitosis in the intestinal cells of isopods observed by Ryder and Miss Pennington, as referred to by Conklin ('97). These were shown by him to be artifacts due to pressure in manipulation and resultant distortion. In that case the amitosis was in adult cells and the pressure was brought about by instruments and not in embryonic tissue and in a course of nature. The food-ova do not compress the endoderm, for at the time they are swallowed the layer has not as yet been formed; they grow out into the cavity after the ova have been swallowed. After a study of the available material I have not been able to resist the conviction that in Fasciolaria we find a true case of embryonic cells multiplying, contrary

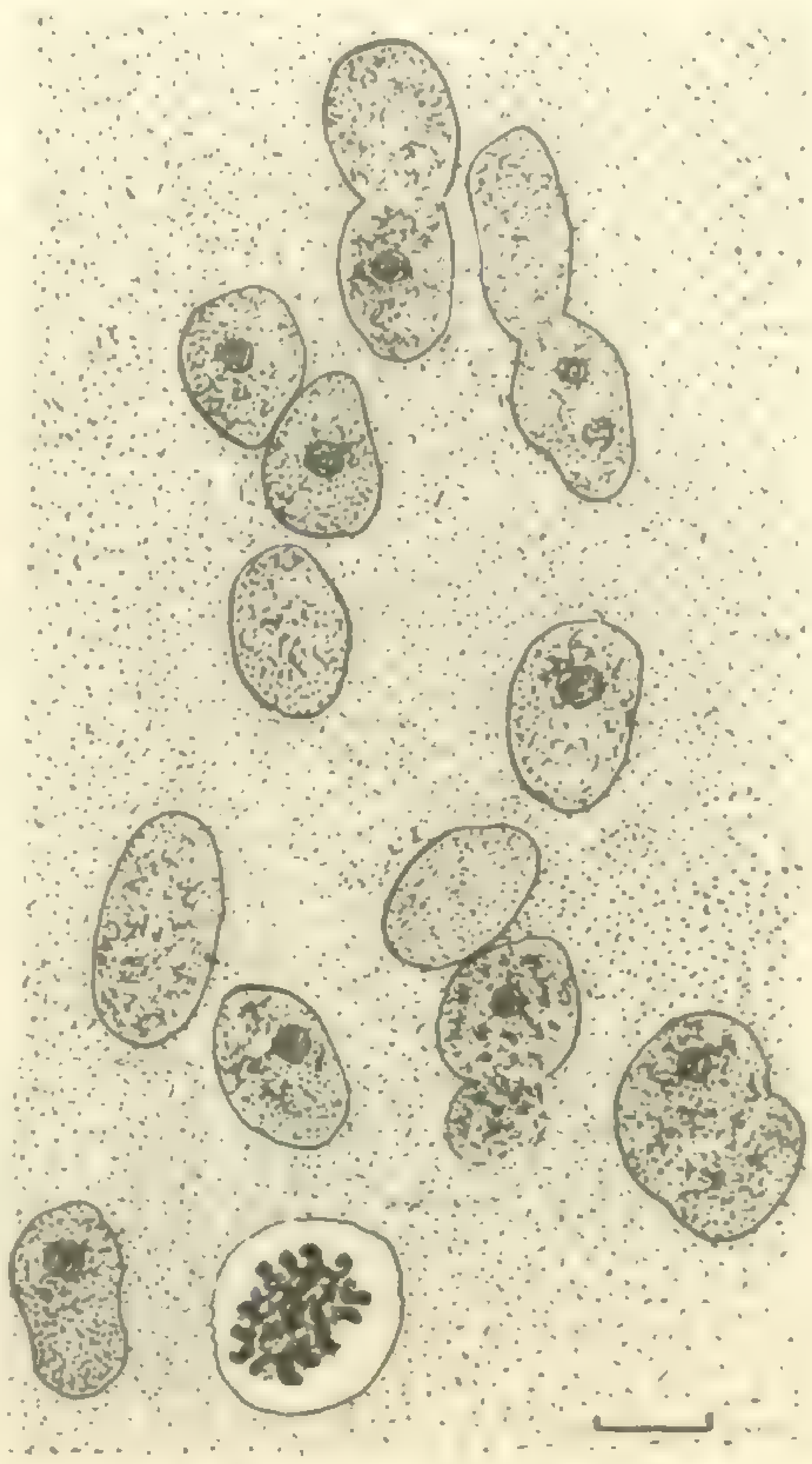

FIG. 11. — Surface view (tangential section) of part of endoderm, showing nuclei in direct division. Scale = .01 mm., cam. luc. × 600.

to the very general rule, by amitosis. A renewed study of this and kindred forms with reference to this point is much to be desired.

These cases of amitosis are sufficiently out of the common order to require a further study in the light of the general principles relating to the amitosis question. That of the larval kidney could perhaps be attributed to senescence but hardly to metabolism, since cells are found dividing by mitosis after secretory activity has been going on to such an extent that the nucleus is distorted and crowded into one side of the cell. The cells after they have reached a stage in which amitosis is found have apparently reached the end of their career and do not multiply further; that is, they are senescent.

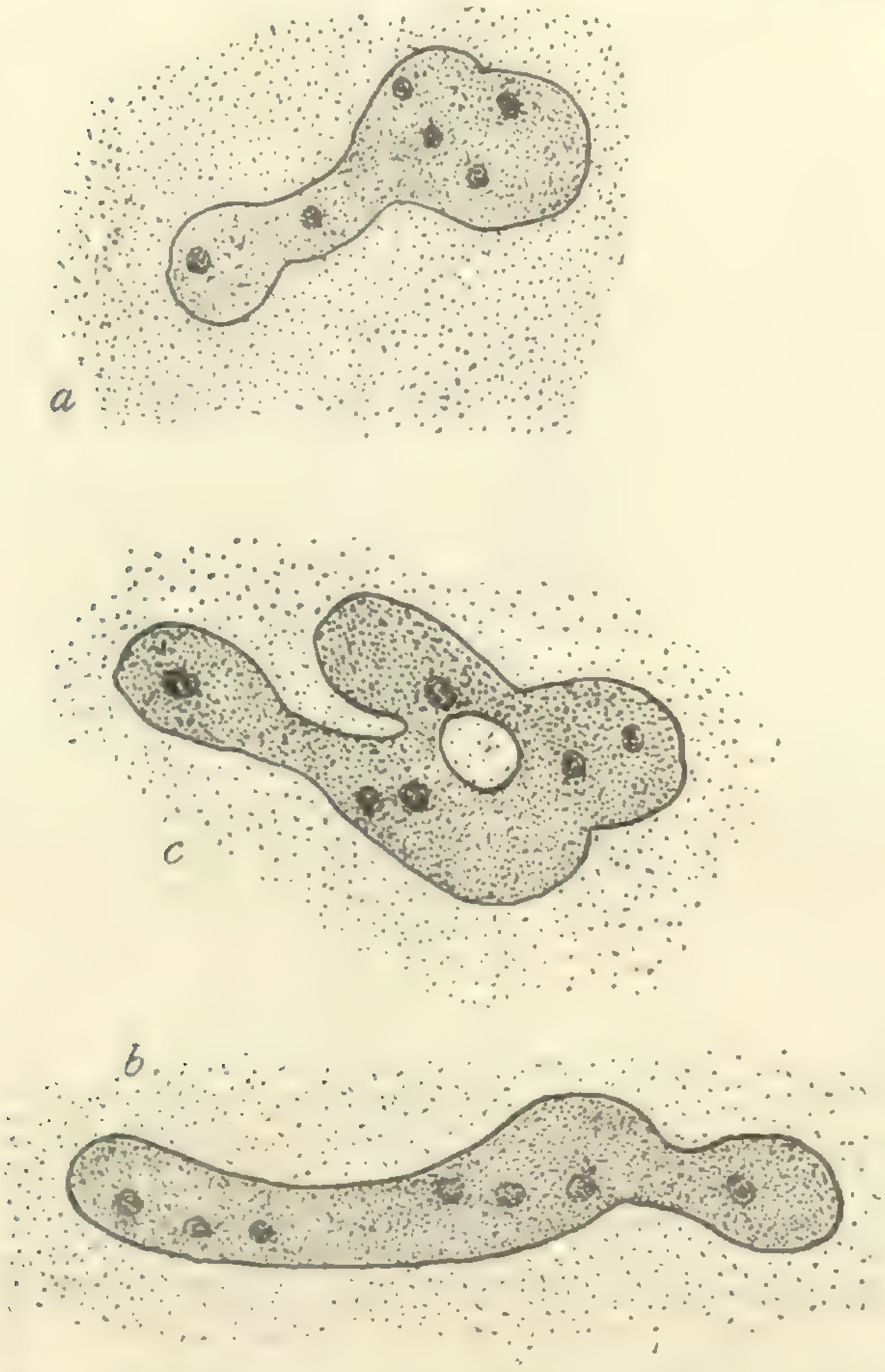

FIG. 12. — Nuclei in the endoderm, plasmodial type, cam. luc. × 600.

It is highly remarkable that the food-ova nuclei should not divide mitotically, for the food-ova are to be interpreted as unsegmented eggs. The divisions of the nucleus in ordinary eggs both in maturation and segmentation are mitotic, and we are justified in expecting karyokinesis of the food-ova nuclei. But instead their nuclei are queer from the first and seem to divide amitotically. This amitosis cannot be assigned to either senescence or metabolism, the cells show no signs of secretory activity, and are not senescent. The case of Spirogyra, according to Pfeffer, and of the salamander, according to Meves, are somewhat analogous in that

in both of them mitosis has been replaced by amitosis through the influence of an extraordinary circumstance, cold weather or ether. We know of no parallel to the case of the food-ova among the gasteropods. In the trematodes the yolk cells of the egg are perhaps somewhat similar; their nuclei do not divide at all.

The nuclei of the young endoderm are also out of the ordinary course. We should expect them to divide by mitosis. While in a small percentage of cases they do divide in that manner, in most cases the indications are strongly in favor of amitosis. Here neither senescence nor metabolism can be the cause of the amitosis. The cells have not yet arrived at their definitive form, much less become old, and secretion has not yet commenced; but, on the contrary, the cells are actively multiplying, so that they quite contradict the theory proposed by Ziegler and vom Rath.

We see, then, that while the amitosis of Fasciolaria can be attributed to senescence in one case, it cannot be attributed to either senescence or metabolism in the other two cases; and in the endoderm the amitosis is even regenerative. We have seen that senescence and metabolism cannot be regarded as causes in certain other instances of amitosis, such as those reported by Fresnel, Meves and Pfeffer. Upon the hypothesis that mitosis and amitosis are independent and non-related processes, cases of this sort are wholly unintelligible, and consequently indicate a defect in the hypothesis, if not that it is erroneous. It is true that we do not find intermediate modes of nuclear division between mitosis and amitosis, and yet *à priori* we should suppose them to be related and mitosis to have been derived from amitosis. The exceptions that are being found are all of them cases in which mitosis would be looked for and amitosis is found. The frequency of mitosis in embryonic tissue does not prove that embryonic tissue cannot multiply by amitosis; it only shows that there is some reason why in most cases it does not. Since mitosis is such a delicately adjusted and complicated process, may we not suppose that a nucleus to be capable of it should be in the best possible condition, — that is, young and vigorous, — and to that end that the surrounding conditions

should be as favorable as possible? And may we not further suppose that in the presence of conditions lowering the vigor of a nucleus, even if it were in a case where we should ordinarily expect mitosis, it would then revert to the more primitive mode of amitosis? We are not unfamiliar with the principle of physiological reversion in organs and tissues. Can we extend the principle to nuclei? If so, all the cases where amitosis occurs in a place where mitosis is expected to occur would perhaps be capable of being brought within its scope. Possibly both senescence and secretion as causes of amitosis could be interpreted in the same way. Thus senescence as a cause of amitosis, as it undoubtedly is, would be in reality due to the lowered vitality of the cell consequent on age. Metabolism perhaps could be supposed to cause it, where there is not at the same time, as in fat cells, milk cells and others, senescence, through the presence of the secretion which may exercise an unfavorable influence on the nucleus chemically. Pathologic tissues would also find an easy explanation on this basis to account for the common occurrence of amitosis in them. Summer by inducing optimal well-being of the cell would put it in condition for mitosis; winter by lowering its vitality would render it unable to divide by mitosis but not by amitosis. Pfeffer's observation on the effect of ether would also fall in line, the cell tending to divide by mitosis but being prevented by the interference with its powers consequent on the influence of the ether. In Fasciola the larval kidney cells while young still divide by mitosis and are consequently vigorous, notwithstanding the presence of considerable metabolic material, but as they become old they lose this power and divide by amitosis. The food-ova with their tendency to mitosis are placed in conditions so unfavorable to their well-being that cell division does not take place at all and nuclear division is only by amitosis. The deeply staining granular particles in some of them may be imperfectly formed chromosomes, as if mitosis had been attempted but without success. A careful cytological study of these food-ova would be very likely to repay study, as it might throw light on the relation between the two modes of nuclear division. The endoderm cells are developing in the amitotic manner and this is the chief

mode by which the embryonic gut enclosure is taking place, if not the only mode. In their case neither senescence nor metabolism can be urged as the cause of the amitosis. Under ordinary circumstances we should find the endoderm increasing by mitosis, but here the mode of growth is very extraordinary, and the case only finds explanation on the principle I have been indicating. I do not know just what particular cause should be assigned in the case of the endoderm, which is to be considered as interfering with the mitosis; perhaps it is the pressure conditions existing in the enteron owing to the presence of such a large amount of inert and foreign matter; perhaps it is the absence of the most favorable food for the endoderm, since the food-ova have not yet begun to be consumed.

Note.— Since revising the last proof of this article, the writer has read with interest a passage in Dr. Davis' article (Am. Nat. 38, p. 434) containing much the same idea vid.— "It is possible that direct division in the higher plants is in a sense a reversion to early ancestral conditions, a reversion *that comes on only when for some reason the normal activities of the germ cell are in abeyance or have ceased.*"

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BIOLOGICAL LABORATORY OF HAMLINE UNIVERSITY,
SAINT PAUL, MINN.
April 25, 1904.

THE TRANSPLANTING OF TROUT IN THE STREAMS OF THE SIERRA NEVADA.

DAVID STARR JORDAN.

THE rivers of California contain four well marked species of trout: (1) The rainbow trout, *Salmo irideus*, in the streams of the Sierra foothills, and in all the streams of the coast range; (2) the steel-head trout, for which the oldest and therefore correct name seems to be *Salmo rivularis*, rather than *Salmo gairdneri*. This is found in the coastwise streams only, whence it runs regularly to the sea, the rainbow trout running only when the sea is conveniently near; (3) the cut-throat trout, *Salmo clarki*, found only in the streams of the northern and northwestern counties; and (4) the Tahoe trout, *Salmo henshawi*, a derivative of the cut-throat found on the east flank of the Sierras, in the tributaries of the extinct Lake Lahontan.

Subspecies or variants have developed from these, especially from *Salmo irideus*. The typical rainbow trout is found in the streams about San Francisco Bay. A slight variant called var. *shasta* is found in the upper Sacramento and in the northern Sierras. With it, but rare, is var. *stonei*, the Nissui trout. In the Kings and Kern rivers is the smaller scaled variety, *gilberti*, and from *gilberti* is descended the dwarf golden trout, var. *agua-bonita*, found only in Volcano (Whitney) Creek on the banks of Mount Whitney, above the high waterfall sometimes called Agua Bonita. The typical Tahoe trout, *Salmo henshawi*, spawns in the streams, but in the depths of the lake is a well marked subspecies of large size spawning in the lake, called var. *tahoënsis*.

The distribution of these species is well made out, but certain anomalies were noticed, especially in the distribution of the Tahoe trout. All these anomalies have been found to be due to transplanting by the hand of man. For the benefit of future students of trout I place these facts on record.

The Stanislaus, Tuolumne and Mokelumne Rivers flowing westward from the Sierra Nevada had in the early days no trout above the falls in their cañons. To these streams the trout were carried over the Divide, and the Tahoe trout is now abundant in the upper waters of these rivers.

For the details of the transplanting of these trout I am indebted to the kindness of Mr. H. S. Blood of Angels, the owner of Bear Valley, at the head of the north fork of the Stanislaus, on the "Toll Road" from the Calaveras Big Trees to Carson Valley.

The earliest plant was made in 1859, the Tahoe trout having been taken from Hope Valley, on the east slope of the Sierras, by the Union Water Company to stock their reservoir at the head of the north fork of the Stanislaus.

In 1861, Abram Ritchie of Big Trees and John Christy of Jenny Lind brought Tahoe trout from Hope Valley and planted them in the head waters of Mokelumne River.

In 1863, H. S. Blood of Angel's and J. C. Curtis of Murphy's brought Tahoe trout from Wolf Creek, Carson Valley, and stocked Highland Lakes, at the head of the Stanislaus.

In 1864, O. S. Boardman of Galt took Tahoe trout from Hope Valley, planting them in the Blue Lakes, near the head of the Mokelumne. At about the same time H. S. Blood, Mark M'Cormick and Herman Tyrie stocked Highland Creek with Tahoe trout from Hope Valley.

The middle fork of the Stanislaus was stocked with Tahoe trout from Walker River, Nevada.

In 1873, Joseph Emery of San Francisco, brought trout from the north fork of the Mokelumne, stocking the Blue Lakes of Amador with the Tahoe trout.

The Tahoe trout was planted in Feather River by Mr. Pratt, founder of the village of Prattsville in Plumas County, the fish being taken from Truckee River.

The golden trout, *agua-bonita*, has been taken from Volcano Creek and successfully planted in Lone Pine Creek, on the east side of the Sierra Nevada.

The rainbow trout, var. *shasta*, has been planted by the State Fish Commission in the Truckee River, where it is now abun-

dant. With it was taken the Sacramento perch, *Archoplites interruptus*. The present writer lately obtained a small specimen of this species from an Indian ditch at Wadsworth, Nevada.

The eastern brook trout, *Salvelinus fontinalis*, has been planted in many California streams, which it seems to find congenial.

A NEW SPECIES OF DIAPTOMUS FROM MEXICO.

A. S. PEARSE.

Diaptomus lehmeri, n. sp.

Cephalothorax, broadest at the middle; with four distinct sutures. The last segment, produced laterally and armed with two prominent spines. The first segment of the abdomen, armed on each side with a strong sharp spine. The first segment of the female abdomen is tapering and about as long as the remainder of the abdomen. The second segment is short, being only one-fourth the length of the third. The furcal rami are almost twice as long as broad, and hairy on both margins in the female (Fig. 1), but on the inner margin only in the male.

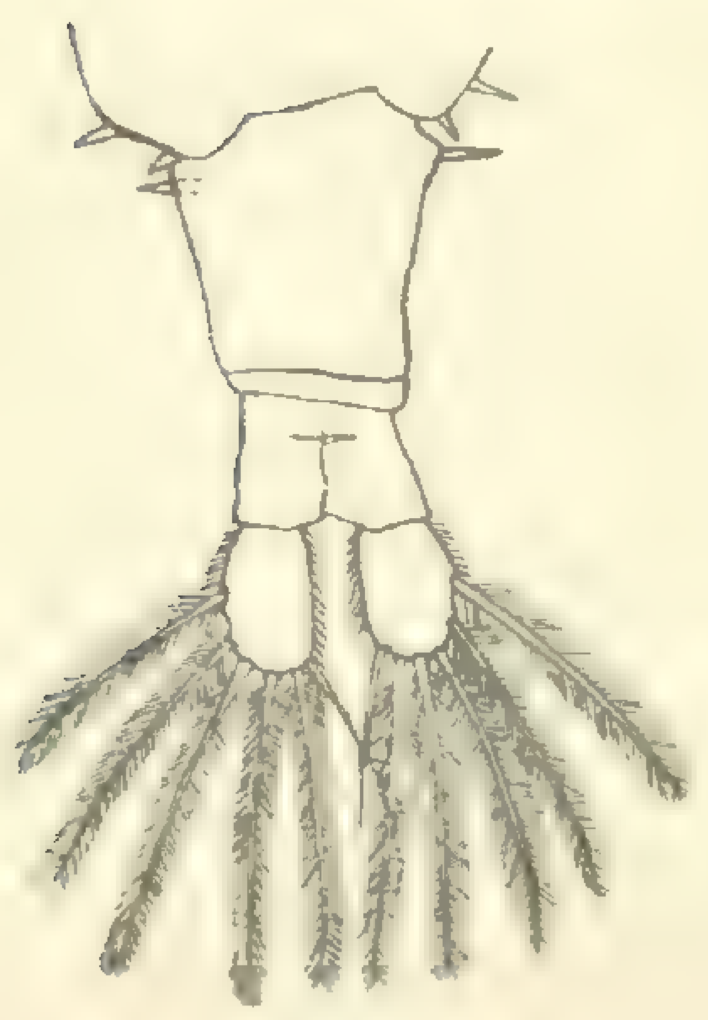

FIG. 1.—*Diaptomus lehmeri* n. sp. Abdomen of female × 87.

Antennæ twenty-five segmented and reaching beyond the tips of the furcal rami. The right male antenna (Fig. 4) is moderately swollen and its antepenultimate segment bears a pointed curved hook, which is not as long as the ultimate segment.

FIG. 2.—*Diaptomus lehmeri* n. sp. Fifth feet of male × 205.

The male fifth feet (Fig. 2) are rather robust. The first basal segment of the right foot has a tubercle near its outer margin which bears a long sharp spine. The second basal segment is almost as

broad as long and besides the usual hair on the outer margin it is provided with a characteristic process on its posterior surface. There is a small hyaline projection on the distal margin of this segment and also on that of the first segment of the outer ramus. The first segment of the outer ramus is very short, being one-third as long as the second segment and is produced into a tubercle at its outer distal angle. The second segment has a large tubercle on its posterior surface. The marginal spine is strong, but slightly curved, longer than the segment, two-thirds the length of the terminal hook, and is roughened on its inner margin. The terminal hook is strong, arcuate and minutely denticulate at the middle of its inner margin. The inner ramus is one segmented, short, (about as long as the first segment of the outer ramus) and hairy at the tip.

FIG. 3. — *Diaptomus lehmeri* n. sp. Fifth foot of female × 205.

In the left male fifth foot (Fig. 2) the first basal segment is armed with a tubercle and spine like that of the right. Second basal segment is three-fourths as broad as long and bears the usual hair on its outer margin. First segment of the outer ramus curved on outer margin, the inner margin notched and ciliated. The terminal segment is triangular and ends in a blunt process and proximad to this is a slender hair; the

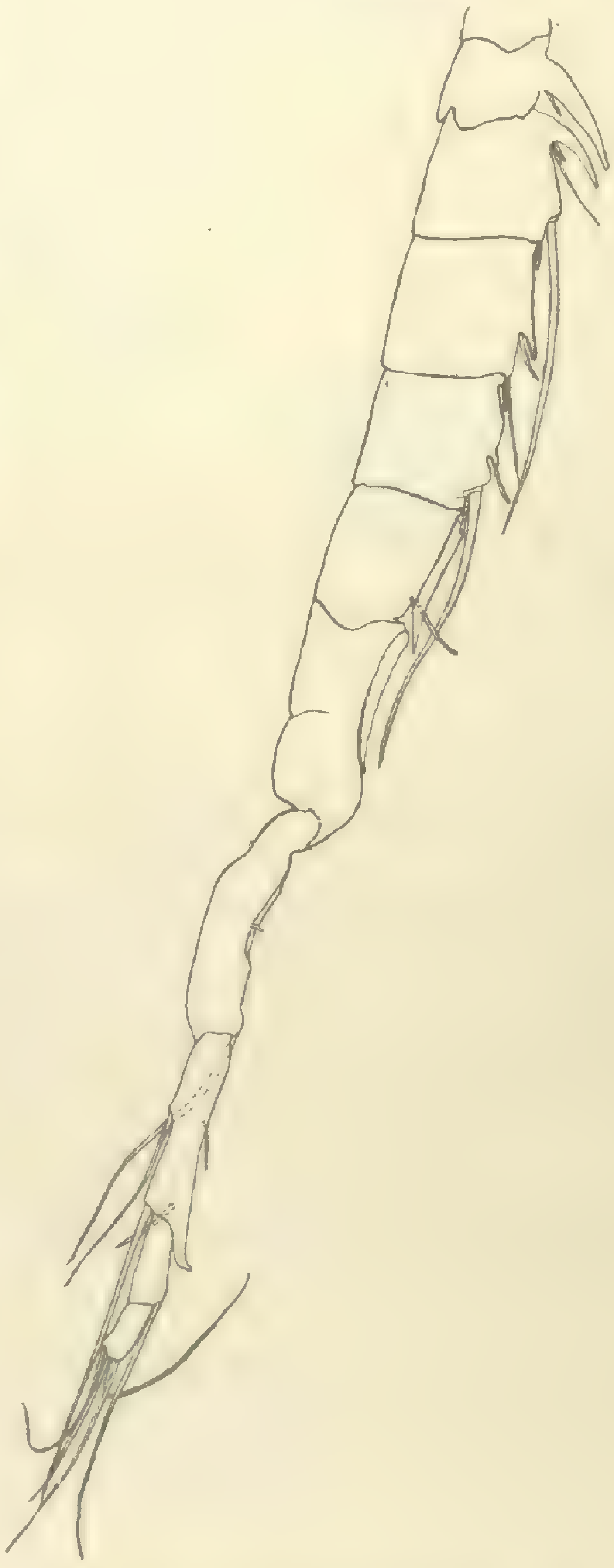

FIG. 4.— *Diaptomus lehmeri* n. sp. Tip of right antenna of male × 128.

inner surface is ciliated. The inner ramus is short and hairy at the tip.

The female fifth foot (Fig. 3) bears a large tapering spine at the outer distal angle of the first basal segment. The second basal segment is triangular and provided with the usual lateral hair. The outer ramus is three segmented. The first and second segments are about equal in length. The second segment is tapering and along the center of its inner side is armed with strong teeth and is usually with two or three small teeth on the outside. The second segment has a short spine above the third segment. The third segment is small and is armed with a long and a short spine. The inner ramus is not half as long as the first segment of the outer ramus and is two segmented. The second segment is armed with two terminal spines with delicate hairs between them and a lateral spine on the inner side.

Length: Female 1.69-1.83 *mm.* Male 1.61-1.67 *mm.*

The specimens from which this species is described were collected by Mrs. Frank Lehmer, July 22 to August 7, 1904, in Mexico City, Mexico. It was apparently abundant at that time, as it occurs in most of the dredgings made.

This species was associated with *Cyclops viridis insectus* Forbes, *Cyclops albidus* Jurine, Canthocamptus sp.?, and an ostracod.

HYLA ANDERSONII AND RANA VIRGATIPES AT LAKEHURST, NEW JERSEY.

WILLIAM T. DAVIS.

On the 5th of last September while looking for insects near a swamp at Lakehurst in the pine barrens of New Jersey, the writer was fortunate in finding a specimen of the rare tree frog *Hyla andersonii* Baird. The frog was in a small oak tree standing but a few feet from the swamp. At the time Cope's work on "The Batrachia of North America" was published in 1889, but three specimens had been recorded, namely the type from Anderson, South Carolina; the one collected at Jackson, Camden Co., New Jersey, in 1863 by Leidy, and the third example found by Dr. John E. Peters at May's Landing, Atlantic Co., New Jersey on June first, 1888. A record of this last is to be found in the *American Naturalist* for January, 1889. In the *American Naturalist* for December, 1894, J. P. Moore gives an account of two of these tree frogs collected in June, 1889, at Pleasant Mills, New Jersey, and of the many others heard at the time. The frogs, however, disappeared shortly and no others could be found on subsequent visits to the locality. Lakehurst is considerably farther North than the three New Jersey stations mentioned above. It may be well to mention at this time that *Rana virgatipes* Cope, is also to be found at Lakehurst. The species was originally described from Cape May County, New Jersey.

According to Cope, in *Hyla andersonii*, "The green of the back and extremities is everywhere margined with pure white, except posteriorly on the femur and tibia, and anteriorly on the former where saffron takes its place." My living specimen, however, differs from this description and the colored figure, by having the band of pure white extend along the end of the body and a short distance on the posterior margin of each femur.

NEW BRIGHTON, STATEN ISLAND, N. Y.

NOTES AND LITERATURE.

PSYCHOLOGY.

Natural Science and Psychology.[1] — For the convenience of those who do not have access to his "Grundzüge der physiologischen Psychologie" Prof. Wundt has reprinted under the above title the last two chapters of the third volume of his great work. In the space of a hundred pages there is given a clear statement of what the author believes concerning: (1) The logical foundations of natural science, (2) Mechanics and energetics, (3) Mechanism and vitalism, (4) Causality and teleology of the psychophysical life-processes, (5) The concept of mind, (6) The principles of psychical causality.

Of special interest to biologists are the discussions of mechanics and energetics, and of the mechanistic and the vitalistic theories. Such a book is valuable to most natural sciences in that it serves to call attention to the too much neglected presuppositions on which specialistic work in the natural sciences rests, as well as to the principles of the sciences. Wundt writes in a patient, plodding, persistent manner; his sanity is all the more evident because of the lack of any brilliancy of treatment.

In view of the appearance of this reprint it is worth while to notice the interest, especially among the German biologists, in the psychic "as an elemental factor in nature," as Driesch in a recent book has stated it. Whether one agrees with Wundt's conception of the relations of the physical and the psychical, with Driesch's, with Ostwald's, with Schneider's may not seem of much consequence to most students of natural science; nevertheless, there can be no doubt that only those who hold theories and see or seek principles can do more than assemble facts whose meaning is clear only in the light of the generalizations which are called laws. No one can study Wundt's book without gaining an interest in the various forms of organic processes that the mere search for facts would not give. To state the content of the book would defeat my purpose to arouse an interest which may lead many to the work itself.

ROBERT M. YERKES.

[1] Wundt, Wilhelm. *Naturwissenschaft und Psychologie.* Leipzig, 1903, 8vo, 126 pp.

"The Criminal Classes."[1] — Rev. D. R. Miller, D.D., has been chaplain of the Ohio Penitentiary and superintendent of the Girls' Industrial Home of Ohio. In "The Criminal Classes. Causes and Cures" he has collected material of various sorts connected with his service in these positions.

At the beginning, near the middle, and near the end of the volume, are chapters briefly treating in a general way the extent of crime, its cost to the community, causes of crime, and methods for the prevention of crime. These discussions are somewhat vague and commonplace and are not fully adjusted to the results of recent scientific study. This sentence from the chapter on "Innate and Psychological Causes" may serve as an illustration of the nonagreement with conceptions of present day physiological psychology: "Regarding moral conduct, in this class there seem to be indications of a broken or missing link between the brain tissues and the moral monitor." There are evidences also of lack of familiarity on the part of the author with recent literature in penology. For instance, he writes, "As agencies in the prevention of crime and the reformation of young criminals, too much importance cannot well be attached to the private and public institutions denominated 'Child-saving institutions,' 'Schools for the little ones,' and 'Homes for children.'" He then fails to mention the movement now in force in many parts of this country, which recognizes that care for children in institutions has not generally prepared them well for life outside of institutions, and which substitutes for the institutional method the methods of probation and placing out, that is, the supervision of the rearing of delinquent and dependent children, while they live as members of their own or other families. Many of the figures on which arguments are based are given without dates but as taken from books and reports now many years old. On the whole these general chapters cannot be said to give an adequate summary of facts known and theories held to-day on the topics which they treat.

A few chapters offer meagre outlines of the careers of noted criminals. Others give brief accounts of the lives and crimes of Ohio convicts. "In the introduction, however," as Dr. Miller says in the preface, "of these narratives, sketches, and illustrations, special care has been exercised to avoid sensational details of the crimes alleged because it is the opinion of the author that all such details serve as

[1] Miller, D. R. *The Criminal Classes. Causes and Cures.* Dayton, United Brethren Publishing House. 1903. 8vo, ix + 227 pp., portraits.

factors to turn into like crime those who may read them." Some of these chapters close with reflections, which, it must be said are in part obvious, in part without special applicability to the cases to which they are attached.

About half the chapters of the book are devoted to incidents that occurred in the author's experience as chaplain, and to writings by prisoners, in prose and poetry, on religious and other topics, some apparently sincere, others with a suggestion of cant. In religious work for the prisoner results can doubtless be gotten easiest by appeals which recall religious instruction received during childhood. At the same time nothing in a man's work as chaplain forces him to adapt himself to changes in religious thought in the world at large. It is natural, therefore, that the weight of the religious interest of the author should be, as it is, such as belongs with religious beliefs of a conservative type.

There is an introduction by Ex-Governor Foster of Ohio. A chapter by Professor Krohn of the University of Illinois compares criminals in whom strange combinations of traits are found with cases of double personality, but fails to call attention to some important differences.

Apparently Dr. Miller is a man who has done earnest and helpful personal work with the criminals placed in his care, but who in his devotion to his own special task has failed to gain the broad acquaintance with current thought in criminology and related subjects which would be needed for writing a very useful book on the causes and cures of crime.

ZOÖLOGY.

Fixation of the Eggs of the Crab. — Dr. H. Charles Williamson, in the 22d *Annual Report of the Fishery Board of Scotland*, adds considerably to our knowledge of the life history of the shore crab of Europe, *Cancer pagurus*. Possibly the most interesting is his discovery of the way in which the eggs are fastened to the swimmerets. These, like other eggs, have double envelopes, the outer chorion and the delicate inner vitelline membrane, and between these a small perivitelline space. When the eggs are extruded from the oviducts they pass into the brood chamber between the abdomen and thorax

and here are held in position by the exopods of the swimmerets while the endopods, covered by slender filiform hairs, extend into the mass of eggs. The pleopoda have powers of motion in two planes, one fore and aft, the other oblique. By these motions the ends of the hairs are brought in contact with the eggs which are thus penetrated by them, the hair passing in and out again. The egg itself rotates and escapes injury. In this way numbers of eggs are impaled or skewered on each hair. As development proceeds the chorion stretches and gives rise to a stalk, which increases in length with time. This process is also aided by the perivitelline fluid, which is adhesive and sticks the chorion to the hair. After the egg is hatched the egg shells and their stalks are cast off by molting the integument, the outer layer of the hairs, together with the adhering shells being cast with the rest of the 'skin.' The eggs are fastened only to the hairs of the endopods, as these alone are smooth and filiform. The hairs of the exopods are plumose or serrate, a condition which prevents their perforating the eggs.

Gardiner's Maldives.[1] — The third part of the second volume of Gardiner's Report maintains the unusually high quality of its predecessors. It contains six papers, of which three are written by members of the expedition and the three others by well known specialists.

The Isopoda are treated by Stebbing in 23 pages. Thirteen species are described, representing eight families. While some are from the sea at moderate depths, two (a Corallana and a Limnoria) are found in rotten wood in the lagoon, one (Cirolana) lives in tentacles of a large tubicolous polychæte. A Cymothoa lives on the gills of a parrot-fish. Tylokepon, n.g., is a bopyrid living on the gills of crustacea. Finally, a sphæromid (Exosphæroma) and a Ligia are representatives of two semi-terrestrial groups.

The Hydromedusæ are treated by Browne. The discussion of the Anthomedusæ leads to a revision of the family Williadæ with two genera, Willia and Proboscidactyla, of which the latter only is in the collection from the Maldives. It occurs also on the east coast of North America and has several species notable for their production of medusa buds. Among the Leptomedusæ is a five-rayed representative of Mayer's genus Pseudoclytia which Browne, following Mayer, believes to have arisen as a sport. The Trachomedusæ are treated in synoptic fashion. A new species and a new

[1] Gardiner, G. S. *The Fauna and Geography of the Maldive and Laccadive Archipelagoes, etc.* Vol. II, part III, pp. 589–698, pls. 35–48.

genus are created. Hermaphroditism is described in one case. One Narcomedusa, a long known species of the Indian Ocean, is described. Five species of Siphonophores were collected. The author states that he could find no copy of the Mark Anniversary Volume in London. Let him apply to Henry Holt & Co., New York.

The reptant decapods of the suborders Hippidea, Thalassindea, and Scyllaridea, are treated by Borradaile. The first two groups are taken between tide marks, the latter in the reefs or on sandy bottom. There are enumerated two albuneids and three hippids (Remipes), one axiid, a gebiid, four callianassas, two palinurids and one Scyllarus.

The Madreporaria are treated by Gardiner, who lays especial stress on their variation, distinguishing vegetative, continuous, and discontinuous or specific. This extensive paper is accompanied by well executed half-tone plates from photographs of the dry corals.

The Antipatharia are described in a few pages by Forster Cooper. They are chiefly Indian Ocean species.

The Arachnida of the archipelagoes, treated by Pocock, raise the question of their origin. "Some of the species, such as Isometrus europæus, Heteropoda regia and Uloborus geniculatus, which frequent human dwellings, have doubtless been introduced by human agency; but it is probable that the ancestors of the majority of the Spiders reached these islands on floating gossamer threads." "The presence of only one species of Scorpion [Isometrus europæus], and that a form notoriously liable to dispersal by man's instrumentality, suggests that, unless in very remote times, there has been no connection between the archipelagoes and the mainland of India . . . . and this is further borne out by the almost complete specific identity between the two faunas."

C. B. D.

CLIMATOLOGY.

Ward's Translation of Hann's Climatology.[1] — Dr. Hann, professor of cosmical physics at the University of Vienna and formerly director of the Austrian Meteorological Bureau, published in 1883

[1] Hann, Dr. Justius. — *Handbook of Climatology. Part I, General Climatology.* Translated by Robert DeCourcy Ward. The Macmillan Company, 1903. 8vo. 437 pages.

his *Handbuch der Klimatologie* which he reissued in 1897 in three volumes. This is the standard work on the subject of climate and no book in the English language is so authoritative or covers so wide a field. Consequently, Professor Ward's translation of the volume relating to General Climatology, which was made primarily for the use of his classes at Harvard University, confers a great boom on all American and English students of meteorology and physical geography.

In his title, Professor Ward has been too modest, for his book is itself revised and enlarged, considerable new matter relating to America having been substituted for certain topics which pertained more particularly to Europe. While it might be wished that this new material were distinguished from the author's German text, it is stated that all the additions have been approved by Dr. Hann, so that the translation is virtually a third edition of this part of the original work. Numerous references to recent periodical and other literature, in various languages, have been added and all the old references have been verified, so far as possible, by the translator. An added convenience is the summary of the contents of each chapter, while a copious index of subjects and authors facilitates looking up either. The metric system and the Centigrade scale of temperature are used throughout and should aid in familiarizing our students with these units, which are destined to supplant the English system in scientific writings. At present, however, the conversion tables in the Appendix will, no doubt, be found necessary by many readers. The German text has been accurately rendered into elegant English, and almost no typographical or other errors have been noted. As was said, only the first volume of Dr. Hann's work has been translated and this evidently possesses the most general interest, since the climatology of special regions, discussed by Dr. Hann in his other two volumes and consisting largely of statistics, can be more easily consulted by persons not familiar with the German language.

In conclusion, the reviewer expresses the hope that this admirable and disinterested work may have a wide circulation in our high schools and colleges and indeed among all English speaking persons who desire to understand the climatic conditions of the globe and their cause.

A. Lawrence Rotch.

BOTANY.

Bog-Trotting for Orchids[1] is the title of a popular book dealing with the swamp flora of the Hoosac Valley. It gives a pleasant, diary-like account of the author's rambles for three seasons, in the course of which are given descriptions and other information regarding her various finds. An appendix of 44 pages presents a systematic account of the genera and species of New England Orchidaceæ, and there is an admirably full index. The illustrations are photographic, many of them excellent; some are colored, not always to advantage, and a considerable proportion are of landscape views or objects other than orchids. As one reads the rambling narrative one cannot but sympathize with the writer's enthusiasm, and is sure to get refreshing whiffs of out-door air. Despite occasional inaccuracies, showing the lack of expert revision. and the inclusion of considerable material of rather more personal than general interest, the book has the charm and value which belong to a faithful record of first-hand impressions, and which will doubtless render it an inspiring help to many amateurs.

F. L. S.

Agriculture for Schools.—Two interesting attempts to meet the demand for instruction in matters of special importance to farming communities, are found in a handbook of exercises edited by Prof. Hays[2] and an elementary text-book by Profs. Burkett, Stevens and Hill.[3]

The hand-book consists of 237 exercises of an eminently practical nature as may be judged from the following sample titles taken at random: Food stored in seeds; Making maps of public roads; Transpiration of water by plants; Teeth of domestic animals; Bowline knot; Sharpening pocket knives; Classes of chickens; Classi-

[1] Niles, Grace Graylock.—*Bog-Trotting for Orchids*. New York, C. P. Putnam's Sons, 1904. xiv + 310 pp., 72 pls.

[2] Hays, Willet M.—*Rural School Agriculture*. Bulletin No. 1. *Exercises in Agriculture and Housekeeping for Rural Schools*. St. Anthony Park, Minn., Department of Agriculture, University of Minnesota, 1903. 12mo, viii + 196. 79 figs.

[3] Burkett, C. W., Stevens, F. L., and Hill, D. H.—*Agriculture for Beginners*. Boston, Ginn & Company, 1903. 12mo, xii + 267, 215 figs.

fication of soils; Crossing corn; Emergencies; Removing ink from white goods; To make liquid yeast; Chicory in coffee; Cash account; Tent caterpillars; Planting trees; Farm gate lesson; Sewed seam; Overhand patch; Three-cornered darn; Cleft grafting. These exercises are arranged somewhat in the order of difficulty and in related groups, but the extent to which they shall elucidate principles or develop general ideas must very largely depend upon the teacher. If skilfully incorporated with other work and their bearings broadly discussed many of these exercises would have real educational value in fitting pupils to meet intelligently the actual problems of rural life.

The text-book proceeds in a more orderly way, establishing general principles and showing their application to problems of soil, culture, protection, selection, stock-raising and dairying. Suggestions for profitable observations or experiments are freely introduced. The illustrations are of unusual excellence, and the style clear and direct. Such a book cannot fail to advance the best interests of practical education in much needed directions. Both books might well be used together.

FREDERICK LEROY SARGENT.

Notes.— André Michaux's "Travels into Kentucky," F. A. Michaux's "Travels west of Alleghany mountains," and Harris's "Journal of a tour northwest of Alleghany mountains," are republished, with annotations, by Thwaites as vol. 3 of his series of *Early Western Travels*, issued by the Arthur H. Clark Company, of Cleveland. It is regrettable that the volume is not provided with an index making its wealth of detailed information available.

A small list of arctic plants is given in Schrader's "Reconnaissance in Northern Alaska," published as *Professional Paper No. 20* of the U. S. Geological Survey.

A polyglot suggestion of amendments to the Paris code of botanical nomenclature, addressed to the Vienna Congress of 1905, has been published by the botanists of the Gray Herbarium, the Cryptogamic Herbarium and the Botanical Museum of Harvard University, under date of June 9.

The annual species commonly referred to Polypteris have been segregated under Rafinesque's generic name Othake, by Bush, in vol. 14, no. 6, of the *Transactions of the Academy of Science of St. Louis.*

Three new exotic orchids ascribed to Rolfe are described by Ames in *Proceedings of the Biological Society of Washington*, of June 9.

Two new Jamaican species of Polypodium are described by Maxon in no. 1374 of *Proceedings of the U. S. National Museum.*

Blakeslee has an interesting note on the sexuality of Rhizopus in *Science* of June 3.

A paper on vitality and germination of seeds, by Duvel, forms *Bulletin no. 58* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

A résumé of ecological work in 1903 is given by Cowles in *Science* of June 10th.

A healthy sane tone pervades an article by Holt on the value of field and herbarium work in high school botany, published in *School Science* for June.

Ecological experiments on *Rumex Acetosella* are described by Transeau in *Science* of June 3.

A critical study of Lepidium is being published by Schinz in the *Bulletin de l'Herbier Boissier.*

A popular account of the native Papaw is given by Viola McCohn in *Country Life in America* for July.

A further list of Eastern species of Cratægus is published by Ashe, under date of June 15, in vol. 20, no. 2, of the *Journal of the Elisha Mitchell Scientific Society.*

Professor Bessey calls attention, in *Science* of June 24, to the early falling of the aberrant lowermost leaves of *Acer Negundo* each year.

The July number of *Arboriculture*, printed on paper made from the wood of Catalpa, contains data as to the availability of this wood for paper purposes.

A review of Californian Polemoniaceæ, by Jessie Milliken, forms vol. 2, no. 1, of the *University of California Publications, Botany*, issued May 10.

Heft 19 of Engler's "Pflanzenreich," is devoted to Betulaceæ, by Winkler.

An account of *Persea gratissima* as cultivated in Florida is published by Rolfs as *Bulletin no. 61* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

A developmental account of Juncaceæ is contributed by Laurent to no. 2–3 of the current volume of *Annales des Sciences Naturelles, Botanique.*

Anatomico-ecological studies of Tillandsia are published by Mez in Vol. 40, Heft 2, of *Jahrbücher für wissenschaftliche Botanik.*

The Germination of Amaryllidaceæ is considered by Worsley in the *Journal of the Royal Horticultural Society* of May.

A reprint of Bradbury's "Travels in the Interior of America," second edition, London, 1819, which forms vol. 5 of Thwaites' "Early Western Travels," contains a list of plants collected about St. Louis and on the Missouri River.

Under the title "Contributions to our knowledge of the flora of the Rocky Mountains," Aven Nelson has collected as a thesis for the Doctor's degree his more important papers published in various journals between 1898 and 1904.

The opening fascicle of vol. 5 of Urban's "Symbolæ Antillanæ" contains revisions of Smilax (by Schulz), Celastraceæ (by Urban), and Sapotaceæ, in part (by Pierre and Urban).

Under the heading "Trabajos de la Oficina de Historia Natural," the Colombian government is publishing a series of papers on the botany of that country, by Cortes.

The first fascicle of vol. 2 of Arechavaleta's "Flora Uraguayana," has been issued by the Museo Nacional de Montevideo, as a part of its *Anales.*

Volume 2 of Wood's "Natal Plants" is completed by the issuance of part 4, dealing with grasses.

No. 28 of the new series of "Contributions from the Gray Herbarium of Harvard University," forming vol. 40, no. 1, of the *Proceedings of the American Academy of Arts and Sciences*, and issued on July 18th, contains the following papers: Robinson and Greenman, Revision of the Genus Sabazia, Revision of the Mexican and Central American Species of Trixis, and Revision of the Mexican and Central American Species of Hieracium; Fernald, Synopsis of the Mexican and Central American Species of Alnus, and Some New Species of Mexican and Nicaraguan Dicotyledons; and Greenman, Diagnoses and Synonymy of Mexican and Central American Spermatophytes.

A companion to M. van den Bossche's "Icones Selectae Horti Thenensis" has been started, also with the botanical collaboration of de Wildeman and the delineating skill of d'Apreval, under the title "Plantæ Novæ vel Minus Cognitæ ex Herbario Horti Thenensis." The first part bears date March, 1904.

An account of the Harvard Botanical Station in Cuba, with extracts from Superintendent Grey's report, is given by Dr. Goodale in *The American Journal of Science* for July.

A quarto treatise on the Phytoplankton of the Atlantic and its tributaries, by P. T. Cleve, is published by the author at Upsala.

A large number of economic topics are well treated by Halsted in his recently issued *Report of the Botanical Department* of the New Jersey Agricultural Experiment Station, for 1903.

An account of the principal commercial plant fibers, by Dewey, is separately printed from the *Yearbook* of the U. S. Department of Agriculture, for 1903.

An illustrated account of some old trees, by Pollmer, is contained in *Die Gartenwelt* of June 25.

Professor Peck's Report of the State Botanist for 1903, published as Bulletin 75 of the New York State Museum, contains among other things a paper on edible fungi and one on the species of Cratægus found in the State.

Experiments in the heredity of peas are detailed by Hurst in the *Journal of the Royal Horticultural Society* of May.

A second edition of E. G. Paris' "Index Bryologicus," reaching to the end of 1900, is being issued in fascicles from the Hermann Press, of Paris.

A further addition to the nomenclature literature to be laid before the Vienna Congress of 1905, by Harms, forms appendix 13 to the current *Notizblatt des K. botanischen Gartens und Museums zu Berlin*, and is dated June 20, 1904.

A bacterial rot of the Calla is described by Townsend in *Bulletin No. 60* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

An account of "fungoid pests of the garden," by Cooke, is contained in current numbers of the *Journal of the Royal Horticultural Society*.

Cultural experiments with biologic forms of the Erysiphaceæ are detailed by Salmon in a paper separately printed from the *Philosophical Transactions of the Royal Society of London*, Series B, vol. 197.

"Investigations of Rusts" is the title of *Bulletin No. 63* of the Bureau of Plant Industry of the U. S. Department of Agriculture, by Carleton.

A paper by Cooke on edible fungi is contained in the *Journal of the Royal Horticultural Society* of May.

The botanical articles of greatest interest in the *Year-book of the United States Department of Agriculture* for 1903 are: — Kebler, "The Adulteration of Drugs"; Taylor, "Promising New Fruits"; Shepard, "Macaroni Wheat"; True, "Cultivation of Drug Plants in the United States"; Dewey, "Principal Commercial Fibers"; and the reports on plant diseases forming part of the appendix.

Vol. 11 of the *Proceedings of the Iowa Academy of Sciences* contains the following articles of botanical interest: — Buchanan, "A Contribution to our Knowledge of the Development of *Prunus Americana*"; Miller, "The Lichen Flora of the 'Ledges,' Boone County, Iowa"; Martin, "A Chemical Study of *Rhus glabra*"; Cratty, "The Flora of Emmet County"; and Mueller, "A Preliminary List of the Flowering Plants of Madison County."

A number of interesting botanical papers are contained in the recently issued Vol. 36 of the *Transactions and Proceedings of the New Zealand Institute.*

Vol. 1 of Rendle's "Classification of Flowering Plants" (Cambridge, 1904) deals with Gymnosperms and Monocotyledons.

An account of Pæonia, as now popularly cultivated, is contributed by Miller to *Country Life in America* for September.

The first part of a discussion of the variability of Eucalyptus under cultivation is published by Maiden in No. 112 of the *Proceedings of the Linnean Society of New South Wales.*

An illustrated account of the cultivation of *Acacia mollissima*, by Fairchild, forms *Bulletin no. 51, part 4* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

Vol. 10, part 1, of the *Annals of the Royal Botanic Garden, Calcutta*, consists of a revision of the species of Dalbergia of S. E. Asia, by Prain.

Opuntia rutila is figured in the *Monatsschrift für Kakteenkunde* of July 10.

Ailantus Vilmoriniana, a Chinese species, recently introduced into France, is described and figured by Dode in the *Revue Horticole* of Sept. 16.

Two segregates of *Rubus argutus Randii* are described by Blanchard in *The American Botanist* of July.

A very large tree of *Quercus alba* is described and figured by Rothrock in *Forest Leaves* for August.

The fruit of Melocanna, a viviparous grass without endosperm, is described by Stapf in Vol. 6, part 9, of the current botanical series of *Transactions of the Linnean Society of London.*

An important paper on monœcious and diœcious grasses, with illustrations, is published by Pilger in Engler's *Botanische Jahrbücher* of August 16.

The aerating nodal roots of Bambusa are discussed by Montemartini, in Vol. 3, fascicle 2, of the *Contribuzioni alla Biologia Vegetale* of the Palermo botanical institute.

The root structure of North American terrestrial orchids is considered by Holm in *The American Journal of Science* for September.

A study of the Corbularia group of Narcissus is published by Bureau in No. 1–2 of the current volume of the *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France.*

A synopsis of the varieties of pineapple cultivated in Florida is given by Hume and Miller in *Bulletin 70* of the Experiment Station of that State.

No. 23 of Holm's "Studies in the Cyperaceæ," published in *The American Journal of Science* for October, deals with morphological aspects of the inflorescence.

No. 2 of *Plantæ Novæ vel Minus Cogintæ ex Herbario Horti Thenensis*, dated in June last, contains a considerable number of Cyperaceæ by Clarke.

An exhaustive paper entitled "Contributions to the Knowledge of the Life History of Pinus with Special Reference to Sporogenesis, the Development of the Gametophytes and Fertilization," by Miss Ferguson, forms a thick brochure of Vol. 6 of the *Proceedings of the Washington Academy of Sciences*, issued on October 4th.

In the *Gardeners' Chronicle* of August 6, Mr. Shaw restores two lost names of Morelet (1855) for later names in Pinus by Grisebach and himself.

A general account of the vegetation of Missouri, by Duggar, is contained in Williams' "The State of Missouri," printed at Columbia, Mo.

A physiographic and ecological study of the Lake Eagle region of Indiana, by Mills, is contained in the 28th *Annual Report* of the Department of Geology and Natural Resources of that State.

Separates of Dr. Kennedy's "Flora of Willoughby, Vt.," have been issued, in attractive binding, by the author, from *Rhodora*.

An account of the flora of the Peace River region of Canada, is given by Macoun in *The Ottawa Naturalist* of September.

Botanical items are included in Notes on the Falkland Islands, by Vallentin, in Vol. 48, part 3, of the *Memoirs and Proceedings of the Manchester Literary and Philosophical Society*, issued in July last.

A "Novus Conspectus Floræ Europæ," by Gandoger, is in course of publication in the *Bulletin de l'Académie Internationale de Géographie Botanique*.

Ascherson and Græbner's "Synopsis der Mitteleuropäischen Flora," in Lieferung 31–2 concludes the Spathifloræ.

Coste's "Flore descriptive et illustrée de la France, etc.," in Vol. 3, fascicle 2 reaches into Polygonaceæ.

The concluding third volume of Halácsy's "Conspectus Floræ Græcæ." has recently been issued from the Engelmann press of Leipzig.

Vol. 4, section 2, part 2, of the "Flora Capensis," under the editorship of Sir William T. Thiselton-Dyer, is occupied with Scrophulariaceæ.

Cooke's "Flora of the Presidency of Bombay," in Vol. 2, part 1, reaches well into Boraginaceæ, — on the Bentham and Hooker sequence of families.

An account of the vegetation of the district of Minbu, in Upper Burma, by Gage, forms Vol. 3, part 1, of the *Records of the Botanical Survey of India*.

A comprehensive biological account of the island of La Mocha, by Reiche and others, forms No. 16 of the *Anales del Museo Nacional de Chile.*

Notes by Bessey in *Science* of July 22 show that each plumed akene of Taraxacum weighs on an average .00044 gm., and that a medium sized tree of *Populus deltoides* bears not far from 28,000,000 seeds, of an average weight of .00065 gm. each.

An interesting paper on the adventitious epiphytic occurrence of terrestrial plants in Norway has been distributed by Holmboe from No. 6 of the current volume of the *Christiania Videnskabs-Selskabs Forhandlingar.*

The thermotropism of Rhododendron is described and illustrated by Johnson in *Country Life in America* for November.

A preliminary paper on electrotropism of roots, by Plowman, is published in *The American Journal of Science* for August and September.

A popular account of carnivorous plants, by Shreve, is contained in *The Popular Science Monthly* for September.

A new and enlarged edition of Pammel's "Flower Ecology" has been published from the J. B. Hungerford Press of Carroll, Iowa, under the title "Ecology." Seventeen chapters deal with the chief topics.

Professor Kraemer has issued separates of a paper on the origin and nature of color in plants from Vol. 43 of the *Proceedings of the American Philosophical Society.*

A note on the pollination of *Calepogon pulchellus* is published by Klugh in *The Ottawa Naturalist* of August.

A syllabus of the economic plants of the temperate zones represented in the Dahlem garden is given by Engler in Appendix 14 of the *Notizblatt des K. botanischen Gartens und Museums zu Berlin.*

A key to the genera of the forest trees of Indiana, based chiefly upon leaf characters, by Coulter and Dorner, has been issued by the authors from Lafayette, Ind.

Under the title "Getting Acquainted with the Trees," a tasty and beautifully illustrated little book by McFarland has recently been issued by The Outlook Company, of New York.

An excellent little illustrated pocket guide to British trees is Step's "Wayside and Woodland Trees" (Warne, London and New York, 1904).

Stone's "Timbers of Commerce and their Identification" (Rider, London, 1904) is a descriptive catalogue — rather than handbook — of 247 species, with phototype illustrations of the wood sections.

The forest resources of Texas are discussed by Bray in *Bulletin 47* of the Bureau of Forestry, U. S. Department of Agriculture; and the forests of the Hawaiian Islands are discussed by Hall in *Bulletin 48* of the same Bureau.

"The Forest Manual," containing the Forest Act (No. 1148), extracts from other laws of the Philippine Commission relating to the forest service, and the forest regulations prepared in accordance with the provisions of the Forest Act, is a little pamphlet recently issued by the insular Bureau of Forestry.

An account of basket willows and their insects is given by Hubbard and Chittenden in *Bulletin No. 46* of the Bureau of Forestry, U. S. Department of Agriculture.

The chestnut in southern Maryland is discussed by Zon in *Bulletin No. 53* of the Bureau of Forestry of the U. S. Department of Agriculture.

Hooper reports on Indian gums yielded by species of Acacia in *The Indian Forester* of September.

A considerable account of Gutta Percha and Rubber is contained, with illustrations, in the recently issued *Report of the Superintendent of Government Laboratories in the Philippine Islands*, for the year ending Sept. 1, 1903.

Economic articles on the Sisal plants and the West Indian anthracnose of cotton [caused by *Colletotrichum Gossypii Barbadense*] are contained in Vol. 5, no. 2, of the *West Indian Bulletin*.

An account of the propagation and marketing of Oranges in Porto Rico is given by Hendricksen in *Bulletin No. 4* of the Porto Rico Agricultural Experiment Station.

An account of the anatomy of edible berries, by Winton, is published in the *American Journal of Pharmacy* for September.

Native ornamental plants of New Mexico are considered by

Wooton in *Bulletin No. 51* of the New Mexico Agricultural Experiment Station.

Nestler, in a pamphlet on "Hautreizende Primeln" (Berlin, Borntraeger, 1904), shows that *Primula Sinensis*, *P. Sieboldii* and *P. Cortusoides* have the poisonous properties now well known as possessed by *P. obconica*, which he finds not shared by *P. officinalis*, *P. megasecæfolia*, *P. floribunda*, *P. Auricula*, *P. capitata*, *P. farinosa*, *P. Japonica*, *P. hirsuta*, *P. Clusiana*, *P. minima* or *P. rosea*.

The cultivation of mushrooms, including the "tissue-culture" growth of spawn, is considered by Duggar in *Farmers' Bulletin No. 204* of the U. S. Department of Agriculture.

An important paper on sexual reproduction in the Mucorineæ, by Blakeslee, forming No. 58 of the "Contributions from the Cryptogamic Laboratory of Harvard University," is published as Vol. 40, no. 4, of the *Proceedings of the American Academy of Arts and Sciences*.

Nos. 15 to 18 of Lloyd's *Mycological Notes* deal mainly with puffballs, especially the typical material of European and North American herbaria.

An article on Uredineæ, with far-reaching conclusions on sexuality, by Blackman, is published in the *Annals of Botany* for July.

An account of *Bacillus violaceus Manilæ*, a pathogenic species, is given by Woolley in *Publication 15* of the Bureau of Government Laboratories of Manila.

An account of *Coniothyrium Diplodiella* is given by Montemartini in *L'Italia Agricola* of September 30.

Conidial fruit of Morchella, similar to if not identical with *Costantinella cristata*, is described by Molliard in the *Revue générale de Botanique* of June 15.

Three fascicles of Lindau's account of Hyphomycetes ("Rabenhorst's Kryptogamen-Flora von Deutschland etc., Vol. 1, Abtheilung 8") have recently appeared.

A continuation of Rehm's "Ascomycetes Americæ Borealis" is contained in the July number of *Annales Mycologici*.

Diseases of Ginseng are discussed by Van Hook in *Bulletin 219* of the Cornell University Agricultural Experiment Station, issued in June.

An excellent series of folio views in the Botanic Garden at Brussels has recently been issued by the Ministère de l'Agriculture of Belgium.

A portrait of Sir Joseph Hooker is published in Vol. 6, part 3, of the *Transactions of the Natural History Society of Glasgow.*

A medallion portrait of A. P. de Candolle forms the frontispiece of Vol. 4, no. 8, of the *Bulletin de l'Herbier Boissier.*

The Journals.—*Journal of Mycology*, May: — Morgan, "*Tubercularia fasciculata*"; Smith, "A New Egg-Plant Fungus [*Ascochyta Lycopersici*]"; Durand, "Three New Species of Discomycetes"; Christman, "Variability in our Common Species of Dictyophora"; Cockerell, "A New Hypholoma"; Clements, "Saccardo, De Diagnostica et Nomenclatura Mycologica, Admonita Quædam"; Kellerman, "A New Species of Næmosphœra [*N. lactucicola*]"; Kellerman, "Minor Mycological Notes — IV"; Kellerman, "Index to North American Mycology" [continued]; Kellerman, "Elementary Mycology" [continued]; Kellerman and Ricker, "New Genera and Species of Fungi Published since the year 1900"; and Kellerman, "Notes from Mycological Literature — X."

Botanical Gazette, June: — Thaxter, "Notes on the Myxobacteriaceæ"; Smith, "Undescribed Plants from Guatemala and other Central American Republics -- XXVI"; Kearney, "Are Plants of Sea Beaches and Dunes true Halophytes?"; Eastwood, "Some New Species of Western Polemoniaceæ"; Peirce, "Notes on the Monterey Pine"; Chrysler, "Anatomical Notes on Certain Strand Plants"; and Allen, "Chromosome Reduction in *Lilium Canadense.*"

Botanical Gazette, July: — Land, "Spermatogenesis and Oogenesis in *Ephedra trifurca*"; Smith, "Water-Relation of *Puccinia Asparagi*"; MacDougal, "Delta and Desert Vegetation"; Arthur, "The Æcidium of Maize Rust"; Livingston and Jensen, "An Experiment on the Relation of Soil Physics to Plant Growth"; and Eastwood, "A New Gilia."

The Bryologist, July: — Fink, "Further Notes on Cladonias — III"; Britton, E. G., "Further Notes on Sematophyllum"; Gilbert, "Mounting Mosses"; and Grout, "*Tortula pagorum* in Georgia."

Bulletin of the Torrey Botanical Club, June: — Salmon, "A Revision of some Species of Ectropothecium"; Murrill, "The Polypora-

ceæ of North America — VII"; Cook, "The Nomenclature of the Royal Palms"; and Osterhout, "Notes on Colorado Plants."

Journal of Mycology, July: — Morgan, "New Species of Pyrenomycetes": Holway, "Notes on Uredineæ — II"; Ricker, "Notes on Fungi — I, New or Interesting American Uredineæ"; Ellis and Everhart, "New Species of Fungi from Various Localities"; Kellerman, "A New Species of Peronospora": Kellerman, "Cultures of Puccinia Thompsonii"; Kellerman, "Elementary Mycology" (continued); Kellerman, "Index to North American Mycology" (continued); Kellerman, "Notes from Mycological Literature — XI"; and Kellerman and Ricker, "New Genera of Fungi Published since the Year 1900" (continued).

Journal of the New York Botanical Garden, July: — Britton, "Explorations in Florida and the Bahamas"; Nash, "Effects of the Past Winter on Shrubs."

Ohio Naturalist, June: — York, "The Embryo-Sac and Embryo of Nelumbo; Kellerman and Jennings, "Flora of Cedar Point"; Kellerman, "Flora of Hen and Chicken Islands, 1903"; and Schaffner, "The Jacket Layer in Sassafras."

The Plant World, June: —Nehrling, "The Beginning of Spring in Florida — III"; Safford, "Extracts from the Note-Book of a Naturalist on the Island of Guam — XIX": Schofield, "The Glumes of 'Beardless' Barley"; and Barrett, "The Lleren, a Rare Root Crop."

The Plant World, July: — Safford, "Extracts from the Note-Book of a Naturalist on the Island of Guam — XX"; Goetting, "On Lonely Rocks and Sand-edged Bluffs"; Shear, "The Black Fungi"; and Bailey, "Some Unusual Woody Plants."

Rhodora, June: — Kennedy, "Flora of Willoughby, Vermont"; Fernald, "Identity of Michaux's *Lycopus uniflorus*"; Eggleston, "Addenda to the Flora of Vermont"; Hervey, "Plants New to the Flora of New Bedford"; Collins, "Some Maine Mosses"; Sheldon, "Some Introduced Weeds of Connecticut"; Robinson, "James Lawrence Bennett"; Knight, "A New Sunflower for Maine"; and Kennedy, "Additional Notes from Willoughby."

Rhodora, July: — Collins, "Some Interesting Rhode Island Bogs"; Deane, "Preliminary Lists of New England Plants — XVII [Polemoniaceæ — Acanthaceæ]"; Fernald, "The Green Alders of New England"; Clark, "An Interesting Specimen of *Arisæma tri-*

phyllum"; and Parlin, "A New Station for *Nyssa sylvatica* in Maine."

Torreya, June:—Campbell, "Resistance of Drought by Liverworts"; Lloyd, "The Pollen Tube in the Cucurbitaceæ and Rubiaceæ"; MacDougal, "Evening Primroses"; Berry, "Teratology of Seedling Bean"; and Britton, "*Scirpus Coloradœnsis* sp. nov."

Torreya, July:—Jelliffe, "Additions to 'The Flora of Long Island'"; Nash, "A Collecting Trip to Haiti"; Berry, "Two-bracted Dogwood"; Britton, "*Savia Bahamensis*, n. sp.; and Shafer, "Notes on Cuban Plants."

Botanical Gazette, August:—Davis, "Oogenesis in Vaucheria"; Billings, "A Study of *Tillandsia usneoides*"; Spalding, "Biological Relations of certain Desert Shrubs. 1, The Creosote Bush (*Covillea tridentata*) in its Relation to Water Supply"; Hitchcock, "Notes on North American Grasses—III"; Perkins, "Carl Schumann" (with portrait); Chamberlain, "A Correction."

The Botanical Gazette, for September:—Chrysler, "Development of the Central Cylinder of Araceæ and Liliaceæ"; Johnson, "Development and Relationship of Monoclea"; Coker, "On the Spores of Certain Coniferæ"; Peirce, "Artificial Parasitism"; and Herre, "Growth of *Ramalina reticulata*."

The Botanical Gazette, October:—Davis, "The Relationships of Sexual Organs in Plants"; Fink, "A Lichen Society of a Sandstone Riprap"; Bergen, "Transpiration of Sun Leaves and Shade Leaves of *Olea Europæa* and other broad leaved Evergreens"; Hitchcock, "Notes on North American Grasses—IV"; Stevens, "Oogenesis and Fertilization in *Albugo Ipomœæ-Panduratæ*."

The Bryologist, September:—Britton, "Hyophila, a New Genus to the United States"; Harris, "Lichens—Stereocaulon, Pilophorus and Thamnolia"; Clarke, "Curbstone Mosses."

Bulletin of the Torrey Botanical Club, July:—Gruenberg and Gies, "Chemical Notes on Bastard Logwood"; Bicknell, "Studies in Sisyrinchium—X. The Species of California"; Cushman, "Notes on Micrasterias from Southeastern Mass."; Rydberg, "Studies on the Rocky Mountain Flora—XI."

Bulletin of the Torrey Botanical Club, August:—Murrill, "Polyporaceæ of North America"; Shaw, "Note on the Sexual Generation and the Development of the Seed-Coats in Certain of the Papavera-

ceæ"; Cannon, "Observations on the Germination of *Phoradendron villosum* and *P. Californicum*"; Griggs, "Two New Species of American Wild Bananas, with a Revision of the Generic Name."

Bulletin of the Torrey Botanical Club, September: — Vail, "Studies in the Asclepiadaceæ — VIII"; Cockerell, "North American Species of Hymenoxys."

The Fern Bulletin, July: — Price, "Contribution toward the Fern Flora of Kentucky"; Clute, "The Star Fern"; Prince, "Some Ferns of the Cave Region of Stone County, Mo."; Eaton, "The California Gold Fern"; Clute, "A New Form of the Christmas Fern"; Eaton, "Is *Asplenium lanceum* American?"; House, "Some Rare Ferns of Central New Jersey"; Parish, "Additions to the California Fern Flora"; Clute, "Raising Prothallia of Botrychium and Lycopodium"; Clute, "Concerning Forms and Hybrids"; Eaton, "*Isoetes Amesii*, a Correction"; Osmun, "*Equisetum variegatum* in Connecticut."

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